

The University of Chicago

DORMANCY AND LEAFING IN
WHITE ELM (*ULMUS AMERICANA*)

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1935

By

GEORGE TALLMAN JONES

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
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INTRODUCTION

During the year 1923-24 the author had contact with work of Dr. Victor E. Shelford on the codling moth in relation to weather. The definiteness of the effect of weather on the time of emergence of the moth from the pupa was very clearly shown. The author was struck by the implication that trees must respond in a very similar way to the same factors of weather as do their insect pests if there is to be any correlation between emergence of the insects and leafing or blossoming of the trees.

The preponderance of deciduous trees in eastern United States demonstrates the fact that the climate is such as to bring about periodic dormancy. The summers are normally so favorable as to enable those trees which are mesophytic during their active life to succeed best, but the winters are so severe that the trees must assume extreme xerophytism and dormancy through the winter if they are to survive. Cold makes food manufacture impossible or of slight amount, and, therefore, the retention of the leaves of little value; it makes water absorption by the roots difficult, so that death from drying might probably result if the leaves were retained; and it kills the trees by direct freezing damage if they are in active condition. Periodic dormancy and resumption of activity are then necessary for the continuance of any mesophytic species in this climate, but such periodicity is obviously of no value except as it is strictly correlated with the rhythm of the climate. If a tree goes into dormancy too soon, it loses some opportunity to make food and may fall behind in growth and in competition with other trees, but if it goes into dormancy too late, freezing damage may be severe. Similarly, if a tree leafs too late, it loses opportunity to make food, and, if it leafs too early, its new leaves may be killed by frosts. One may speak of this strict correlation between the rhythm of the climate and the rhythm of the organism as the organism being geared to the rhythm of the climate. A different climate induces a difference in the gearing of the organism. It is a matter of common experience that many west European plants are not hardy in eastern United States because they begin to leaf too soon. In western Europe, the oceanic climate makes late freezes very much less likely than in eastern United States, with its continental climate. In some way it takes a greater mass of warmth in the spring to bring about

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leafing of our native trees. This necessity for accumulation of a greater mass of warmth means delay, and, because of our late freezes, there must be delay if freezing damage is avoided.

An investigation of dormancy and leafing would appear to consist of four main questions: What are the factors that bring about (a) the assumption of dormancy and (b) the breaking of the rest period, (c) what is the effect of favorable weather before leafing, and (d) what mass of favorable weather is necessary before dormancy is completely broken.

A number of investigators have worked on the problem of the rest period and assumption of dormancy in plants. W. L. Howard (32), 1915, defines the rest period as "that period during which plants are, for the most part incapable of responding to growing conditions." The dormant period is understood to be the period from normal leaf fall in autumn until the beginning of leafing or flowering in the following spring. As a rule, the white elm enters its rest period in late June and abandons it in December, whereas the elm enters its dormant period in late October and abandons it in late March. That is, stem lengthening and cambial activity cease in early summer and normally will not be resumed again that season, but the tree will respond to conditions suitable for growth in January, though actual leafing will not occur for two or three months thereafter.

W. L. Howard (32), 1915, felt that winter can bear no relation to the rest period, because the rest period begins while two or three months of good growing conditions still remain. Strausbaugh (64), 1921, however, thinks that adaptation to seasonal variation must be a much more profound matter, since, obviously, those plants which do not develop a method of safe dormancy are eliminated from our habitat. Abbott (2), 1923, suggests that the rest period rhythm is probably due to the inheritancy of an internal set-up from a long line of successfully adapted ancestors, and that the plant is kept in conformity with the annual rhythm by reaction to the periodic repetition of external stimuli. It hardly seems possible that any sort of internal set-up could continue to keep a plant in correct conformity with the annual rhythm in the absence of external stimuli. In fact, MacDougal (44), 1930, found that *Juglans major* retained its leaves and continued growth from two to three times the normal period, when transplanted to a region of continuous warmth. On the other hand, external stimuli alone cannot possibly account for the rhythm shown by plants, for plants vary so markedly under identical external conditions. The author has frequently noted the fact that the last leaves put out by a tree during unusually prolonged growth are retained for weeks after the rest of the leaves have

fallen. Lamb (38), 1915, reports that a soft maple tree put out new leaves after being heavily pruned in August, and that these leaves were retained till December, though others were dropped in October. The problem would then appear to be a dual one of internal physiology and external stimuli.

The problem of internal physiology in relation to rest and dormancy does not fall within the scope of this paper. Suffice it to say that the seat of the phenomenon seems to be in the buds rather than in any other tissue. Denny and Stanton (16), 1928, found that a single bud of *Syringa vulgaris* could be chemically stimulated into activity without any corresponding response in untreated buds.

Relatively little has been published on the problem of what external stimuli induce dormancy. Progressive chilling and shorter day length are two of the most dependable factors of climate associated with approaching winter. Cold-hardiness is not the same thing as dormancy, though the two do bear a rather close relationship. However, much more work has been done on cold-hardiness, and, since the two do bear so close a relationship, it may be that a study of the factors that induce one may throw some light on what induces the other. Dexter (17), 1933, found that those things favor cold-hardiness which favor accumulation of carbohydrates. Warm days and cold nights seem particularly effective, and that is the normal weather condition in autumn. Frost is not necessary for the assumption of dormancy by plants, nor is it always beneficial. During several autumns of late years there has been no frost until November, and yet the elm leaves were dropped during October.

Since the classical work of Garner and Allard (26), 1920, on length of day in relation to plants, much work has been done on a great variety of aspects of the length of day problem. Allard (4), 1932, says, "Length of day rhythm may determine distribution of plants by preventing fruiting or interfering with preparation for unfavorable conditions of the habitat." This suggestion that length of day may have something to do with dormancy is supported by Moshkov (47), 1930. He found that under long day illumination *Robinia pseudo-acacia* continued growth and was frost killed, whereas under short day it accumulated carbohydrates and developed cold-hardiness. Work already published would, then, suggest that a combination of shortening day and alternation of warm days and cold nights is responsible for the assumption of dormancy by deciduous trees.

The physiological condition of plants during dormancy has been the subject of investigation by a number of workers. Howard (33), 1915, held that "rest sets in on account of the inhibition

insects as these are given by Sanderson and Peairs (54), 1913, Shelford (56), (57), and others.

The physico-chemical experiments suggested the application of Vant Hoff's law of Q_{10} . This law of Q_{10} is much used in physiological experiments and has repeatedly been applied to growth and phenological problems. It is based on the observation that chemical reactions are approximately doubled in speed for each rise in temperature of 10° C. In such cases $Q_{10} = 2$. Livingston and Livingston (42), 1913, felt that Vant Hoff's law held for considerations of plant geography, and that a Q_{10} of 2.0 to 2.5 was a fundamental principle of physiology. They worked out a set of temperature efficiency indices by assuming 40° F. as unity and a Q_{10} of 2. These indices were much used for a time, but now seem somewhat divorced from experimental data. The idea of a Q_{10} has

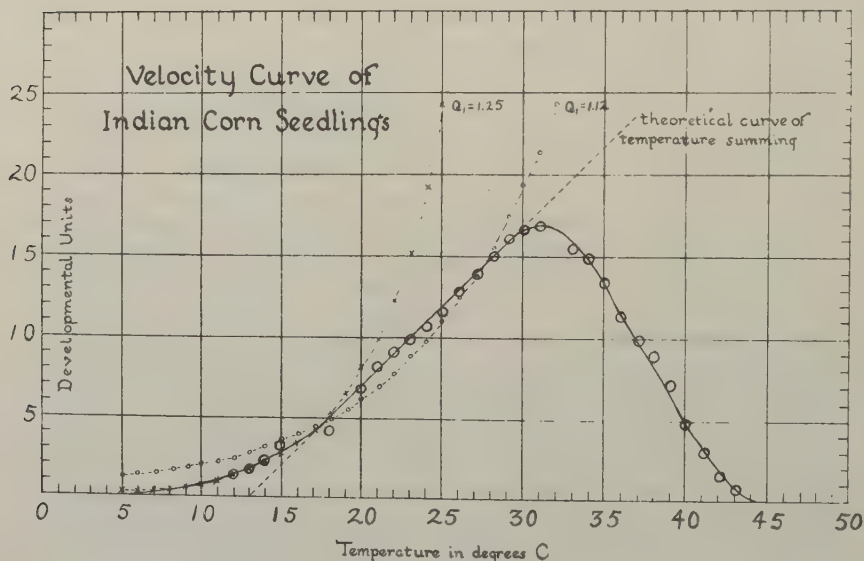


Fig. 1--Redrawn from Shelford. Data from Lehenbauer.

lost favor with those who have worked on growth or development problems, because it does not seem to be a constant. One quite commonly comes across the statement in a physiological experiment that Q_{10} varies as one goes from one end of the effective

temperature scale to another. Evans (22), 1922, in an experiment on the germination of *Amaranthus* seeds, found that Q_{10} varied from over 3 at low temperatures to less than 1 at high temperatures. To the author's mind, this is just another way of saying that in such experiments the law of Q_{10} does not apply. Belehradek (6), 1930, states that the complexity of chemical constitution makes good use of Vant Hoff's and Arrhenius' laws impossible, and that co-efficients of physiological processes are indicative of the viscosities of reacting protoplasmic phases. Shelford (57), 1929, shows graphically that the Q_{10} curve diverges widely from the development curve. In Figure 1 this lack of agreement is shown.

Most of those who have worked on the effect of temperature on living things have noted a lower end point--a point on the scale below which no temperature is effective and above which temperature summation work 0° C. was usually assumed as this lower end point, but most of the physiological experiments have demonstrated the falsity of the assumption. Von Oettingen (48), 1879, used the term "threshold" as the temperature at which development or response barely becomes perceptible. The term is now applied in a similar sense to a great variety of other factors than temperature, and it is a very useful concept. Such a great variety of different temperatures have been found to be the thresholds for different plants and for different activities of the same plant, that the use of one standard threshold, as that by Livingston and Livingston (42), is a source of serious error. Kendeigh (36), 1932, states that the threshold for seeds varies from 0° C. or lower to 9° C., and an even greater range has been noted. Shelford (57), 1929, gives considerable data on the matter of thresholds and the effects on development of differences in thresholds. It is clear, then, that a special study must be made of the actual threshold of each plant studied if the results are to have meaning.

If it is true that temperature is not the only factor that is operative in bringing about growth or development, what are the other factors that are? Various things have been suggested. Lamb (38), 1915, lists as factors which might make a difference in flowering or leafing time; soil conditions, competition with other plants, and amount of stored food. Shelford (56), 1926, found that the relative humidity of the air had such a marked effect on codling moth pupae, that he had to include it with temperature if he was to make accurate predictions of the emergence of the moths. Shelford (56) found, too, that variable conditions produce greater progress toward emergence than do constant conditions of the same averages, and, he felt also that the number of times the pupae were wetted by rain made a difference in time of emergence. Light has been suggested as a factor of influence in

the more far-reaching was the significance to them of signs of Spring. The variation in the earliness of spring in relation to calendar dates has always made it impossible to carry on agricultural operations in strict conformity with the calendar. The natural result is close observation of a variety of natural phenomena which indicate the degree of the advance of spring at any one time, and the growth of proverbs to indicate to the farmer the proper sign for the proper agricultural operation. "Plant corn when oak leaves are the size of a squirrel's ear" is an early New England proverb in point. Becquerel (5), 1853, reviews the history of this development and cites regularly prepared agricultural calendars based on signs of the advancement of spring as far back as 700 B. C. in China, as well as a great many other such ancient to modern calendars. Between 1750 A. D. and 1800 A. D., many European investigators studied the phenomena of the return of Spring, a study they called phenomenology or phenology. A great many records were kept, and much work was done in an endeavor to explain the difference in dates of leafing and flowering of a given plant in different years. It had long been noticed that warmer seasons mean earlier seasons, and warmth would seem to be the chief factor in producing earliness; perhaps, if one could add up all the warmth of winter and spring, one would reach a constant total for each of the happenings of spring. On more or less this assumption many investigators, starting with Reaumur in 1735 (see Shelford (57)), have summed all positive temperatures from January first until the leafing or flowering of the plant in question, with the expectation of reaching a constant total for that activity of that plant--a total that would be the same for all years. As late as 1914, Lamb (38) held to this assumption. However, long before 1914, this summation method had fallen into general disrepute because the sums so attained were not constant but varied greatly--especially so in unusual years. This method of interpretation of the problems of the return of spring had broken down, but interest in the problem continued and many people all over the world continued to keep records of phenological dates. Abbe (1), 1905, and Lamb (38), 1915, cite a long series of records of this sort. Smith (62), 1915, edited and published the records kept by Thomas Mikesell at Wauseon, Ohio, whose records are among the most extensive ever kept in point of time and of the number of species represented.

In recent years there has been a recrudescence of interest in the summation method. As Kendeigh (36), 1932, defines it, "Summation of temperatures is an idea based on the belief that the same stage of vegetation is attained in any year when the sum of mean daily temperatures reaches the same value." MacDougal (43),

1902, tried to increase the speed and precision of summing temperature areas on a thermograph record, but this improvement still possessed the fundamental errors of the method. F. Shreve (61), 1914, pointed out that it is an impossible assumption that one degree on the temperature scale is equivalent to a degree at another point on the scale, and that any explanation of the phenomena of life based on a single factor is fundamentally faulty. He suggests that soil and atmospheric moisture are also very important. Seeley (55), 1917, in working over Mikesell's data found that summation totals for different years for corn and peach disagree from 38 per cent to 78 per cent. It is quite clear that the summation method is inadequate, but what specifically is wrong with it? In the first place, temperature, though perhaps the chief factor, is not the only one, as Shreve (61), 1914, and Shelford (56), 1926, point out. Secondly, the values of temperatures on different parts of the temperature scale are quite different from their assumed values, and they vary from organism to organism. Shreve (61), 1914, states this, and Shelford, in a series of publications (56), (57), (58), (59), demonstrates beyond question the lack of correspondence between the summation curve and the actual curve of temperature effects. Thirdly, the assumption that all temperatures down to 0° C. are effective is untrue, and, as Kendeigh (36) shows, the point on the scale where temperature begins to be effective varies greatly from organism to organism. And, fourthly, no one can tell without experiment on what date summing should begin. The selection of January first is purely arbitrary. There is no evidence that the beginning of a new calendar year has any biological significance.

Approaching the problem from quite a different angle are a great variety of physiological temperature experiments. Lefebure (39), 1801, incubated radish seeds at several different temperatures and recorded the time to germination. His results were in fairly close agreement with those of recent workers. Sachs (53), 1860, conducted a series of similar experiments on a variety of seeds, and it is to Sachs that we owe the terms optimal, maximal and minimal as applied to the physiological effect of temperature. Much other such work was done on seed germination (see Edwards (20)) and on the speed of simple physico-chemical processes at different temperatures, but Lehenbauer (40), 1914, was about the first to carry on an adequate series of experiments on the effect of different temperatures on the growth of plants. His work on maize seedlings is one of the classics. Figure 1 gives the curve of the velocity of growth of maize at different temperatures as Shelford (57), 1929, worked it out from Lehenbauer's data. It corresponds in all fundamentals with the development curves for

of enzymic activity due to over-accumulation of the products of their work," and that respiration and enzyme activity continue at a reduced rate, that they gradually remove the surplus, and dormancy is gradually lost. Strausbaugh (64), 1921, found that the earlier and more complete the maturity of buds, the greater was the winter hardiness. Further, that the hardy species show a minimum of water in the buds with very little fluctuation due to temperature changes, whereas semihardy species contain more water in their buds and show marked fluctuation in water content as temperature fluctuates. In his work with apple and peach seedlings Abbott (2), 1923, found that the rest period begins with increased acidity and increased carbohydrate, and that it ends with reduced acidity, reduced carbohydrate and increase of phosphorus and nitrogen. This would seem to agree with the work of Kraus and Kraybill (37), 1918, which demonstrated that a relative excess of carbohydrate over nitrogen suppresses growth, whereas a relative excess of nitrogen over carbohydrate stimulates vegetative growth. During dormancy, then, the buds would appear to be well stored with reserve food and to be in such a condition that enzyme activity is slight.

As the winter advances, something certainly happens to break this condition of rest and to make it possible for the buds to respond to conditions suitable for growth. What is it that brings about this change? It is not merely a matter of time and good growth conditions, for Adams (3), 1925, found that *Acer saccharum* remained in dormancy in spite of continuous light and high temperatures over a long period, and Gardner (24), 1929, with pear shoots brought into the greenhouse in early autumn, failed to get any appreciable leafing, even after eleven months of good external conditions. Many investigators working on seeds have found that exposure to cold is a necessary condition to germination. To mention only two instances, Doerfel (18), 1930, found that intermittent cold works better than freezing in breaking the dormancy of various seeds, and Giersbach and Crocker (28), 1932, found that wild plum seeds after-ripen at about 5° C. in five months, and that without exposure to cold there is no germination. Work on shoots and seedlings has been less extensive. Coville (8), 1920, and Gardner (24), 1929, both found that exposure to cold was necessary before leafing could begin. Coville (8), felt that freezing was necessary, but Gardner (24) found that a long exposure to only a moderately low temperature may be as effective in breaking the rest period as a shorter exposure to a lower temperature. This necessity for exposure to cold before leafing is illustrated practically by the observation of Horne, Weldon, and Babcock (31), 1926, that the winters of 1904, 1924, and 1926

were so mild in southern California that peach trees leafed very poorly and crop failure resulted.

Experimentally, a variety of other stimuli have been used to break the rest period in plants. In 1906, Johannsen (35) discovered that ether would break dormancy in woody plant twigs. Gardner (24), 1929, lists: warm baths, nutrient salts, narcotics, anaesthetics, woundings, freezing and thawing, and exposure to low temperatures. He gives no evidence as to how these stimuli are effective, but suggests that changes in permeability or enzyme activity may be responsible. Coville (8), 1920, in his work on blueberry, thought that cold is effective in breaking dormancy by the chilling of the vital activity of the cell membranes and a resulting leaking through of enzymes which change starch to sugar. Later workers have felt that the increase of enzyme activity is due rather to a change in the chemical substratum to a state more favorable to enzyme action. Eckerson (19), 1913, in her work on *Crataegus* seeds found that during after-ripening there was a progressive increase in acidity, water holding capacity, and catalase and peroxidase activity. Pack (50), 1921, in his investigation of the chemistry of after-ripening and germination of Juniper seeds, obtained evidence, from the type of chemical compounds which increased in the seeds as after-ripening progressed, that the rapid accumulation of simple plastic cell materials, coupled with a minimum respiration and combustion of materials probably forces the dormant organs into activity. Denny (13), 1932, showed that the chemicals that induced sprouting of previously dormant potato tubers increased amylase activity in proportion, but in 1933 (14) he found that there is no simple relation between the chemicals that break dormancy and amylase activity, and he stated that breaking of dormancy is not just stimulation of amylase activity. Denny and Miller (15), 1932, in studying the effect of ethylene chlorhydrin vapors upon dormant lilac tissues discovered that under such treatment there was much increase in catalase, some increase in bud moisture, soluble nitrogenous substances, respiration and invertase, and a decrease in sugar. This again correlates with the carbohydrate-nitrogen relation as shown by Kraus and Kraybill (37), 1918. The consensus of opinion seems to be that exposure to a temperature of about 5° C. over a period of some weeks is necessary if the condition of dormancy in most of our deciduous plants is to be broken.

The question of the effect of favorable weather on the renewal of activity in dormant plants has been one of great interest to the inhabitants of a climate like ours since the earliest times. The more immediate the dependence of people on the renewed activity of food plants and on the associated return of migratory animals,

this connection, but no actual data has been presented to demonstrate its effect on leafing or blossoming time.

Whatever the effective factors may be, there are many occasions on which it is desirable to know how far along toward leafing or emergence an organism is at a given time, and to do so, it is obvious that some method of adding together totals of progress during good weather is necessary. It has been shown that direct summing of temperatures will not yield dependable results; the summing of units of actual progress would seem to be the only satisfactory method. But how is this to be done?

In trees well adjusted to our climate, there appears to be the need of the experience of a certain mass of conditions suitable for growth before leafing can occur and growth actually begins. This mass of good growth conditions has been assumed to be a constant total and is referred to as the thermoconstant, even though it may be dependent on other things as well as temperature. When and only when the thermoconstant total has been reached, leafing will begin. We may assume that a certain portion of this thermoconstant will be accumulated under any given set of conditions and time. If, for each day, we can determine how large a fraction of the "thermoconstant" has been accumulated and can add together such fractions day by day, we will know how far development has gone, and we will be able to predict with considerable accuracy when leafing will occur. Livingston and Livingston (42) tried to do this with their temperature efficiency indices, but on too theoretical a basis, as pointed out above. Livingston (41), 1916, tried again with his physiological indices based on Lehenbaur's maize data, but again his method proved unsatisfactory, because the reactions of no one plant can safely be assumed to be the same as those of another plant, and further, maize, on which the whole thing was based, is peculiar among plants of our region in that it demands an unusual degree of warmth before development begins and its optimum temperature is high. Livingston himself recognized several errors in the method, but felt that it was the best available at the time. In any organism the proportion of progress toward the thermoconstant under different conditions of weather can be accurately determined only by extensive experimentation with that organism. Shelford (56), 1926, in his work with insects, states that 6,000 to 10,000 pure strain individuals in at least sixty experimental combinations were necessary if reliable results were to be obtained. The experimental combinations must include all the factors found to have an influence on the time of leafing or emergence.

At this point, the question arises, what shall these units of progress be called? The old "degree-day" unit is so closely

associated with temperature summing as to be confusing in any other use. Shelford (58), 1930, after trying out a series of less satisfactory terms, settled on "developmental unit" and defined it as, "the difference between the amount of development taking place in one hour at any one degree of medial temperature and that at a temperature one degree higher," it being understood that corrections are made for the effect of other factors than temperature. This definition is very exact but perhaps somewhat difficult to understand without an intimate acquaintance with velocity of development curves. Stated in more homely terms, a developmental unit is a corrected degree hour. Reference to Figure 1 will show a more or less middle portion of the velocity curve in which each degree higher on the temperature scale is equivalent to one additional unit of the vertical speed of progress scale: $20^{\circ} = 7$ units and $21^{\circ} = 8$ units. This directly proportional part of the curve is the medial portion. Both below and above these medial temperatures the curve shows that temperatures do not have this unit for unit relation. For example: 40° is not 20 units more effective than 20° , but is only as effective as 18° . But since development does not begin at 0° , even 18° is not equal to 18 units. Eighteen degrees and 40° are both just as effective as though the threshold were 13° , and in effectiveness for maize, these two temperatures are both only 5° above the zero point and their effectiveness is only 5 units. Obviously 40° for an hour cannot be given any other value than its corrected effectiveness of 5 developmental units.

In resume, it would appear from previous work on this subject, that, to gain an understanding of why the white elm leafs on different dates in different years, it will be necessary to experiment with many plants of a single strain of white elm under a great variety of conditions. The threshold of time, or the time in the winter when the tree first begins to respond to conditions suitable for growth must be worked out; the various factors of weather that influence speed of development must be found with their thresholds and optima for the species; and the thermoconstant or the total mass of good growth conditions between the threshold of time and actual leafing must be determined.

MATERIALS AND METHODS

This investigation was begun in 1928 and carried on until the May of 1935. Of this time, the year 1931-32 was spent in residence at the University of Chicago with this problem the thesis subject; during the other seven years the work was carried on as research during teaching at Oberlin College.

The white elm (*Ulmus americana* L.) was selected as the species for study because it seemed thoroughly adjusted to the rhythm of our climate and was locally common; it fruits abundantly, and the seeds germinate readily early the same summer, so that seedlings are easily obtained; and it blossoms very early and blossoms well before it leaf. To reduce errors due to variations in the plants studied, a single tree, that usually blossomed and leafed at a medial date among members of the species, was selected as the tree of the experiment and seeds from it only were used as a source of experimental plants. The seeds were collected when ripe, usually during the last of May, were immediately planted in flats, and transplanted to pots as soon as about four foliage leaves had formed. For the first three years, single plants were grown in four inch pots, but during the rest of the time of the experiment six inch pots were used with four seedlings to a pot. This was done to reduce space and to increase the similarity of conditions for groups of seedlings. Each pot was numbered both on the pot and on a label stick, and a 4 x 6 filing card was assigned to it for records. Altogether about 2,500 individual seedlings were studied, and, of these, about 700 of the Oberlin plants were carried to Chicago for study there. For comparative purposes, seedlings from seed Dr. H. C. Cowles sent to the author from the neighborhood of Chicago, were grown and studied, but though no great difference from the Oberlin plants was noted, the results from the Chicago plants were not used in the construction of the velocity of development curve. For evidence on flowering and to check evidence presented by others using the method, cut twigs of the experimental tree were used, but did not prove very satisfactory. In addition to the investigation on seedlings and twigs, observations were made as to the time of blossoming and leafing both in the experimental tree and in the species as a whole.

The facilities for this experiment at Oberlin were none too good; the long time the investigation has taken has been due largely to the impossibility of obtaining any considerable series of different conditions during the same period. Adequate greenhouse bench space was always to be had, but with no greater control of conditions than is usually to be met with in an ordinary greenhouse. A hygrothermograph was kept in constant operation in the midst of the potted plants in the greenhouse from October to May during three years of the experimental work there. A daylight lamp and dark room were available for use in the greenhouse whenever desired. A bench was constructed outside one of the north laboratory windows for study of the effect of outdoor conditions on the potted seedlings. The bench was filled deeply with soil and the pots sunk to the rim in the soil, as was always done with pots left outdoors. A maximum-minimum thermometer was in operation in the middle of this bench. For controlled temperature, there were available a deKhotinsky constant temperature incubator with a Bristol recording thermometer, a Thelco Electric Incubator with Bristol recording thermometer, and a Frigidaire of special construction with a Bristol recording soil thermometer. The Frigidaire had one of the stock doors replaced by a special door with a large glass window of three layers of glass, and there were two apertures in the body of the refrigerator for insertion of the bulb of the soil thermometer. In the latter two of these instruments, the temperature varied about one degree on each side of the mean.

At the University of Chicago, the apparatus was much more extensive, but was in such constant use that little of it was available to the author. In the greenhouse where most of the plants were kept, some control of temperature was maintained, except as spring advanced. Daylight lamps, a dark room and thermographs were available, and the constant temperature cold rooms with incubators in them made it possible to run experiments at constant temperatures quite impossible to obtain at Oberlin.

In planning an attack on the problem of dormancy and leafing, the author laid out the following points for investigation:

1. Is dormancy brought about by: (a) chilling or freezing, (b) weak light or short day, (c) age of the leaves, or some other factor?
2. Is after-ripening necessary, and if so, what conditions hasten it or delay it and when is it completed?
3. Must there be a shock to break the rest period, and if so is the shock (a) freezing, (b) low temperature, (c) increase in day length, or what, and will exposure to various vapors work?

4. What factors of good growth conditions are necessary for dormancy to be abandoned? Warmth is a factor, but is:
(a) light, (b) relative humidity, (c) wetting by rain,
(d) soil moisture, (e) soil temperature?
5. In white elm, what is the threshold of temperature and of other factors?
6. What are the relative speeds of development under different conditions?
7. What is the thermoconstant, or the mass of accumulated good growth conditions necessary before (a) blossoming,
(b) leafing?

RESULTS AND DISCUSSION

Dormancy

The white elm is a species well adjusted to our yearly rhythm of temperature by its periodically recurring periods of activity and dormancy. This adjustment is absolutely necessary for the survival of the species here, but what is it that brings about the assumption of dormancy? As brought out in the introduction, the indications are that the assumption of dormancy is due to an inherited internal physiological set-up kept in gear with the rhythm of the climate by response to periodically recurring external stimuli (Abbott (2)). The author's concern in this paper is not the internal physiological set-up, but the external stimuli to which the internal set-up responds by carrying the plant into dormancy.

In the selection of factors for study in the problem, it seemed reasonable to the author to select those regularly recurring factors of climate that most dependably precede the onset of disastrous cold, and to test such factors for responsibility for the assumption of dormancy by the white elm. Frost is often mentioned as responsible for dormancy, but the trees are clearly prepared for cold before frosts occur in autumn, for a frost of no apparent effect in September would cause extensive damage to leaves and twigs if it occurred in late June. Furthermore, twice during the eight years of the experiment no frost occurred until late in November, and the leaves had fallen nearly two weeks before. Frost, then, cannot be the primary determining factor.

In the latitude where the experiments were carried out, the white elm showed the beginning of extensive leaf yellowing from late September to the middle of October, and the trees were bare by October 17 to November 11. Other factors than frost which occur with regularity about or before this period are: progressive cooling, periods of warm days and cool nights, reduction in light intensity, and a shortening of day length. Of these by far the most dependable is the last, shortening of day length. The work of Garner and Allard (26), 1920, and of Allard (4), 1932, and of many others shows that plants do respond to length of day, and day length decreases progressively from the time of cessation of stem elongation in June until complete dormancy is established in

December. Length of day is a factor well worth experiment. None of the other factors are so dependable. Reduction in light intensity is so dependent upon cloudiness as to seem unsafe as an indication that winter is coming. A period of warm days and cool nights appears to be influential when it occurs, for it does increase cold-hardiness as Dexter (17), 1933, found. And progressive cooling also might assist in bringing about dormancy, though cool days earlier in the season have no such effect.

The experiments to test the effect of various factors on assumption of dormancy were carried on largely at Chicago. During October, potted seedlings of the same summer were placed under a series of conditions. Table I gives the results.

TABLE I
FACTORS EFFECTING THE ASSUMPTION OF DORMANCY

Temperature C	Length of Day in Hours	Average Time in Days Till Leaf Fall	Remarks
5 ± 3	8.5	21	Young leaves were retained.
4 ± 3	Darkness	22	Leaves good green when dropped.
5 ± 3	18	92	At 90 days, and accidental light freezing occurred and the leaves were soon dropped.
20 ± 5	11 decreasing	42	Some plants retained their leaves
20 ± 5	18	150	over a year.
Outdoors	11 decreasing	16	Leaves dropped before frost.

Plants in active growth when placed in cold and short days, stopped growth without normal ripening of the apex, but, though the older leaves dropped in 21 to 24 days, the younger leaves remained in fresh condition on the plant for 66 days or until the close of the experiment. The bulk of the greenhouse plants were kept from October through December in a greenhouse adjacent to the long day greenhouse, but the intensity of the extra light they received was so low that no interference with the normal early December leaf fall was expected. However, when it was

found that practically all the leaves were retained into January, the plants were moved to a greenhouse out of reach of long day lamps, with the result that leaf fall was practically complete within a week.

It was not found practicable to carry out experiments on progressive cooling nor on warm days combined with cold nights. However, the greater speed of leaf fall outdoors than in cold and short days, would indicate that one or both of these factors must have an influence. A considerable study was made of the Mikesell data from Wauseon, Ohio (Smith (62)) in an attempt to obtain a solution for the problem of these two factors, but with rather meager results. Several factors must be involved and the statistical methods of multiple correlation would be necessary to prove much, but the records are too few to yield results of any value by those methods. However, it appeared to the author that on the average leaf fall occurred sooner with earlier leafing the previous spring, and with severe drouth, but the author could find no correlation with any other factor--least of all with the time of the first killing frost. In connection with the effect of cooling, it should be noted that greenhouse plants which had dropped their leaves normally in November, as well as plants still in leaf, were always killed when suddenly moved outdoors into sub-zero weather. Harvey (29), 1930, found that white elm was cold-hardened best by subjection to cold or intermittent cold. On the other hand, the results of Moshkov (47), 1930, on black locust indicate that neither chilling nor intermittent cooling produce cold-hardiness in long day, but that they must be combined with short day to prevent winter-killing. Dormancy is clearly not the same thing as cold-hardiness, but both are necessary for survival in our climate.

From the evidence obtained, it seems clear that the most important external stimulus inducing dormancy in white elm is short day. Chilling and alternation of warm days and cold nights would appear to have a contributing but less fundamental effect in inducing dormancy, but to be vitally important in preparing the plants for winter by inducing cold-hardiness. However, since young leaves do not respond to these external stimuli, it is evident that the physiological state of the plant is involved as a predisposing cause. A period of about three months seems to be necessary, after stem elongation has ceased, for the physiological changes to occur that make possible quick response to the external stimuli inducing dormancy and cold-hardiness. This three months is the period defined by Johannsen (35), 1906, as the period of early rest. During this time meristems do not ordinarily respond by growth to conditions suitable for growth, but under unusual

conditions, may be induced to do so. The twigs or plants which do continue growth well into the summer or autumn do not readily respond to short day or cold, do not become safely dormant, and may suffer from winter killing. The cessation of growth while three months of good conditions for growth still remain, a seemingly anomalous situation when plant competition is considered, seems to be necessary in the adjustment of the plant to the annual rhythm of this climate. The supposition that the age of the tissues is partly responsible for leaf fall is borne out by the observations of Holttum (30), 1931, on periodic leaf fall about Singapore under continuous growing season, and is at least suggested by the Wauseon data mentioned above in which time since leafing the previous spring seemed almost the only positive factor in determining the time of leaf fall.

It would appear, then, that short day, cold nights combined with warm days, and chilling as external stimuli acting on physiologically mature plant tissues are responsible for the assumption of dormancy in white elm.

After-ripening and Breaking Dormancy

It has been observed by nearly all who have studied the problem of dormancy in seeds or twigs, that there is usually a period of time after dormancy has set in, during which the seed or bud fails completely to respond to conditions suitable for growth. This is the period referred to by Johannsen (35), 1906, as the "midrest." Then, after a certain time has elapsed or certain conditions have been experienced, the seed or bud, more or less abruptly, begins to respond to environmental conditions of the kind that make growth possible. The period of beginning response is what Johannsen called the "afterrest." Different experiences seem to be necessary to induce the abandonment of dormancy by different plants.

In an effort to discover what stimuli are necessary to induce abandonment of dormancy by white elm, potted seedlings were placed under a variety of conditions, indoors and out. Of the plants always in the greenhouse and never chilled nor shocked in any other way, as far as known, about 2 per cent leafed in March or April, 10 per cent leafed during the summer, and 88 per cent failed to leaf at all. In the absence of any true leafing, there were several cases in which the bud scales were forced apart by the continued formation and accumulation of embryo leaves and associated stem but quite without internode elongation. Flemion (23), 1932, found much the same thing with unafter-ripened *Rhodotypos* seeds. Cold in some form is evidently necessary, since

plants brought in from outdoors after the middle of January leafed very well. However, since the effect of outdoor conditions acts slowly and the time to leafing is progressively longer as the plants are brought in earlier, it seemed desirable to find some other awakening experience that would act with greater rapidity.

A number of plants were exposed to different concentrations of ether, and it was found that 0.5 cc. per liter of air for 24 hours was quite satisfactory, though in that concentration terminal dominance is destroyed and all of the buds of a seedling leafed together. (See Plate I B.) This destruction of terminal dominance is in agreement with the results of Denney (11), 1926, in the effect of thiourea on potato tubers. Exposure to 1.0 cc. of ether per liter of air for 24 hours was tried but found to be too strong, for it killed the buds that would ordinarily come into leaf and brought out the lower ones. (See Plate I A.) It was necessary to do the gassing with these concentrations in a sealed chamber, if positive results were to be obtained. Exposure to ether was found to be a satisfactory means of bringing greenhouse plants into leaf without the time and bother of prolonged chilling, and it yielded some interesting results, but since it is not a natural stimulus and the experiment was intended to demonstrate the external stimuli responsible for leafing under natural conditions, experiments with gassing were not continued. It is a point of some significance that the greenhouse plants that were exposed to ether progressively later in the season leafed in progressively less time, and that their buds opened approximately with those of ungassed plants brought in from outdoors just as gassing was done. Some physiological change due to elapsed time must be going on in the buds, without experience of cold, that, when exposure to ether has shocked the buds into activity, makes accumulation of experience of warmth more and more efficient.

Another and unintended experiment with gassing was carried out by the greenhouse staff during the author's absence. Fumigation with calcium cyanide ($\text{Ca}(\text{CN}_2)$) to kill insect pests was done as a matter of routine while those using the greenhouse for experiments were away, without it occurring to anyone that undesired results might follow. When all the greenhouse plants reserved as checks began to come into leaf, together, without any known shock, the author was perturbed. Investigation brought out what had occurred, and another effective gassing agent for white elm was demonstrated. Cyanide was already well known as an effective stimulating agent for a number of species of woody plants, from the work of Gassner and Robien (27), 1928, and much other work by Gassner, but they used hydrogencyanic acid (HCN). Many other vapors have been used with good results, as by Denney and Stanton

(16), 1928, and Denney (12), 1928.

Other stimuli tried were the hot water bath, a method found very effective for bulbs, and wounding in various ways, which latter is a method suggested as effective by Gardner (24), 1929, from his experience with pear twigs. Neither of these were found to be satisfactory stimuli. With the hot water bath, no combination of time and temperature of the bath produced any result. Some of the seedlings wounded by the tip being cut back did come into leaf, but so irregularly and uncertainly as to be of no value for the purpose intended.

Though it was evident from the results with greenhouse and outdoor plants that cold in some form is the effective agent in breaking dormancy in white elm, it was not clear whether freezing is necessary. In the climate of Chicago and Oberlin, freezing normally occurs during the period before the midrest is over, but that is not of itself proof of its necessity. To clear up the question, potted seedlings were placed in the refrigerator at $5^{\circ}\text{C.} \pm 2^{\circ}$ in November before the leaves had fallen. Care was taken that the temperature should never drop to 0°C. After two months, the plants were transferred to 20°C. and leafed very well and together in six days. Freezing is clearly not necessary for breaking dormancy in white elm. Though this line of investigation is very promising, it has not so far been possible to do more with it, because of other demands on the equipment.

The implication in the above experiment that after-ripening is a matter of accumulation of experience of temperatures around 5°C. is in line with the results of many workers on seed germination. Rose (52), 1919, Pack (49), 1921, Davis (10), 1930, and Giersback and Crocker (28), 1932, all found that the seeds they were investigating, after-ripened best with prolonged experience of temperatures around 5°C. Pack found freezing and thawing to have no value and most of the others state that freezing is not necessary. The result of Doerfels (18), 1930, indicated that intermittent temperatures of 0° to 5° alternating with 30° were most effective with a number of seeds, and that freezing was not necessary, but intermittent temperatures would appear not to be needed by white elm.

In every series of experiments where plants were brought in from outdoors at different dates, it was strikingly clear that the effect of warmth in producing leafing was much less, early in the season than later. This difference was so great that comparison of speed of development experiments on different dates was difficult and of doubtful accuracy. In 1933, an experiment was set up to bring out this matter clearly and to make possible corrections of effective temperatures for time of year, and so make the

comparison of results in different experiments more accurate. Table II gives the experiment and its results. Abbott (2), 1923, got very similar results with potted peach seedlings handled in much the same way.

In Table II, the term "DU" means developmental units, as defined by Shelford (58), 1930, or "the difference between the

TABLE II
EFFECT OF PARTIAL AFTER-RIPENING
ON TEMPERATURE EFFICIENCY

Brought From Outdoors into 20° C. on	Mean Day When Leafing Began	Number of Days at 20° C. Before Leafing Began	Uncorrected DU in 20° C.	Uncorrected DU Outdoors Before 20° C.	Uncorrected Total DU
Nov. 21, 1933	Never			00	
Dec. 8	3/5 never to 2/5				
	Mar. 29	277	73,100	00	73,100
Dec. 18	2/5 never to 3/5				
	Mar. 13	142	37,500	00	37,500
Jan. 2, 1934	Feb. 13	43	12,330	285	12,615
Jan. 15	Feb. 9 P.M.	25.5	6,832	314	6,946
Feb. 1	Feb. 12 P.M.	11.5	3,036	516	3,552
Feb. 14	Feb. 24	10	2,640	523	3,163
Mar. 1	Mar. 7 and 8	6.7	1,769	691	2,460
Mar. 15	Mar. 20 and 21	5.5	1,452	801	2,253
Mar. 22	Mar. 27	4.8	1,267	908	2,175
Apr. 1	Apr. 5	4	1,056	1146	2,202
Apr. 5	Apr. 8 P.M.	3.4	898	1304	2,202
Apr. 9	Apr. 12	2.9	766	1456	2,222

amount of development taking place in one hour at any one degree of medial temperature and that at another temperature one degree higher." The value of the developmental unit has been determined by experiments set forth in a later section of this paper. The developmental unit totals given in Table II represent the mass of effective warmth necessary to bring about leafing in plants with the amount of experience of cold that was theirs before they were brought in from outdoors. It is obvious that the developmental

unit totals need correction by some factor representing the degree of after-ripening that had occurred before the plant was placed in the incubator. Computation of the corrective coefficients was rendered difficult by the fact that, as the season advanced, more and more effective warmth had accumulated outdoors.

But, before anything could be done in the matter of determining the coefficient of correction for after-ripening, it was necessary to find what proportion of complete after-ripening had been accumulated on each date. Though experiment had demonstrated that 5°C . causes rapid after-ripening in white elm, no data is available to show how efficient each temperature around that point may be. It was found necessary for practical purposes to construct a purely theoretical curve of the efficiency of after-ripening temperature in order to have some standard from which to compute the daily increment. This curve was constructed on the basis of the usual curve of temperature efficiency and to the best of the author's judgment. It may be greatly in error. However, the curve is given in Figure 2.

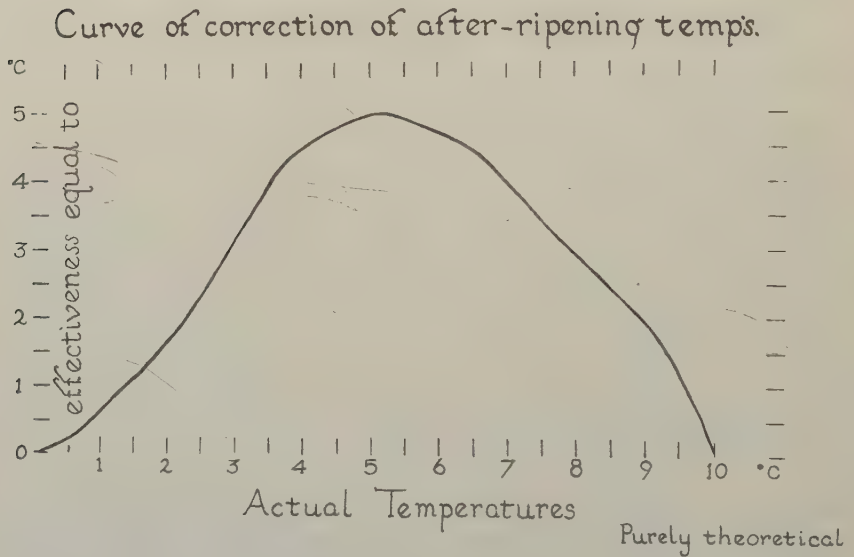


Fig. 2

From the curve in Figure 2 were obtained values of the presumed efficiencies of different temperatures in causing

after-ripening. By using these values, hour by hour totals of after-ripening temperature were determined from thermograph records for each day from December 1 to April 9, as is shown in Table III. In making these totals, if 6:00 A.M. were 2.5° its efficiency

TABLE III

SHOWING START OF CORRECTION OF TEMPERATURE EFFICIENCY IN PROPORTION TO THE DEGREE OF AFTER-RIPENING

1. Brought Into 20° C.	2. DU in 20° C.	3. DU Outdoors Before 20° C.	4. Accum. Mass of 5° C. Outdoors Since Dec. 1	5. Items in IV Per Cent 3,000	6. First Correction of Outdoor DU	7. Total DU to Leafing: First Correction	8. Effic. of DU%: First Correction 1,500 DU Total
Nov. 21		00	00	0	00		0
Dec. 8	73,100	00	160	5.3	00	73,100	2
Dec. 18	37,500	00	410	13.7	00	37,500	4
Jan. 2	12,330	285	815	27.2	62	12,392	12
Jan. 15	6,832	314	1230	41.0	72	6,904	22
Feb. 1	3,036	516	1760	58.7	173	3,209	45.5
Feb. 14	2,640	523	1915	63.8	177	2,817	53
Mar. 1	1,769	691	2345	78.2	299	2,068	73
Mar. 15	1,452	801	2535	84.5	390	1,842	81.5
Mar. 22	1,267	908	2750	91.7	484	1,751	86
Apr. 1	1,056	1146	2935	98.0	713	1,769	85
Apr. 5	898	1304	3125	100.0	875	1,773	84.5
Apr. 9	766	1456	3305	100.0	1067	1,833	82

equivalent of 4.5 would be substituted, for 7.0° would be substituted 4.0, for 9.0°, 2.0, and so on for all the hours of the day, and then all 24 of the values summed to be the total for that day. These daily totals were accumulated day by day to show how far after-ripening had gone under outdoor conditions up to each date. The accumulated totals are hereafter referred to as the

"accumulated mass of 5° C". The day by day accumulated masses of 5° C. are also shown in Table III.

In an effort to determine the coefficient of correction for after-ripening, these accumulated masses of 5° C. were used in conjunction with the experimental data shown in Table II in the construction of Tables III and IV. From the data, it appeared

TABLE IV

COMPLETION OF CORRECTION OF TEMPERATURE EFFICIENCY IN
PROPORTION TO DEGREE OF AFTER-RIPENING

1.	2.	3.	4.	8.	9.	10.	11.	12.
Brought into 20° C.	DU in 20° C.	DU Outdoors Before 20° C.	Accum. Mass of 5° C. Outdoors Since Dec. 1	Effic. of DU % First Correction	Second Correction of Outdoor DU	Second Correc- tion: Total DU to Leafing	Second Correction of DU % Effic.	Third Correction of DU % Effic.
Nov. 21		00	00	0	0		0	0
Dec. 8	73,100	00	160	2	0	73,100	2	2
Dec. 18	37,500	00	410	4	0	37,500	4	4
Jan. 2	12,330	285	815	12	24.2	12,357	12	12
Jan. 15	6,832	314	1230	22	29.0	6,861	22	22
Feb. 1	3,036	516	1760	45.5	100	3,136	48	48
Feb. 14	2,640	523	1915	53	103.4	2,743	58	58
Mar. 1	1,769	691	2345	73	211.0	1,980	76	77
Mar. 15	1,452	801	2535	81.5	297.0	1,749	86	88
Mar. 22	1,267	908	2750	86	387.0	1,654	91	94
Apr. 1	1,056	1146	2935	85	480.0	1,536	98	99
Apr. 5	898	1304	3125	84.5	619.0	1,517	99	100
Apr. 9	766	1456	3305	82	749.0	1,515	99	100

that 3,000 units was the necessary mass of accumulated 5° C. for the completion of after-ripening in white elm seedlings. Column 5 was, therefore, computed as the per cent of 3,000 units of 5° C. that had accumulated up to the time the plants in question were

brought indoors. If the curve of correction for the effect of after-ripening proved to be a straight line, then the values in column 5 would represent nearly the true values. However, the values are too high, as is shown by computation. If the developmental units accumulated outdoors before the plants were brought in (column 3) are corrected by means of the coefficient in column 5, the results in column 6 are obtained. But when these corrected developmental units are added to the developmental units accumulated in 20° C. (column 2) and the totals (column 7) are divided into 1500, very different coefficients result. Fifteen hundred is taken as the total of corrected developmental units necessary for leafing in white elm seedlings, because the plants etherized in late March and the plants after-ripened in the refrigerator all gave approximately that total. Though the values in column 8 are clearly close to the correct values for those near the zero end of the scale, they are even more clearly incorrect for the upper range. The process must be gone through at least twice more to obtain results that seem satisfactory. In Table IV, we have in column 9 the values of the outdoor developmental units corrected by the coefficient in column 8. These, added to the values in 20° C., give the totals in column 10, and a division of these into 1500 gives the per cent of effectiveness shown in column 11. The values are still too small at the top, but a repetition of the process gives the values in column 12, and these appear to be satisfactory. From the per cents of efficiency of developmental units under different degrees of after-ripening, as given in column 12, Figure 3 was constructed. Figure 3 is the curve of correction for the effect of after-ripening. It was found, as will be pointed out later, that adult trees required a larger mass of accumulated 5° C. before after-ripening was completed. It was found possible to determine the curve from the rather unsatisfactory data on cut twigs, and so, for purposes of checking the results from outdoor records of leafing time, a parallel curve with the end point at a greater total was drawn.

As is later pointed out, it was found necessary to correct for degree of after-ripening in order to bring the thermoconstant totals for the natural leafing of the trees in different years anywhere near agreement. Correcting the developmental unit values by coefficients as given in Figure 3 is successful in bringing this agreement about. This fact would strongly suggest that the suppositions involved in the construction of the curve are near the truth.

It is often assumed that the breaking of dormancy is an abrupt change and that the accumulation of warmth or other good conditions proceeds at full value from that moment. The results

here presented demonstrate that this is not true in the case of white elm, and, in fact it is hard for the author to see how there could be so abrupt a change in the physiological condition of the organism when no fundamentally new and different condition has occurred. If after-ripening is a matter of prolonged experience

Curve of Correction for the Effect of After-ripening

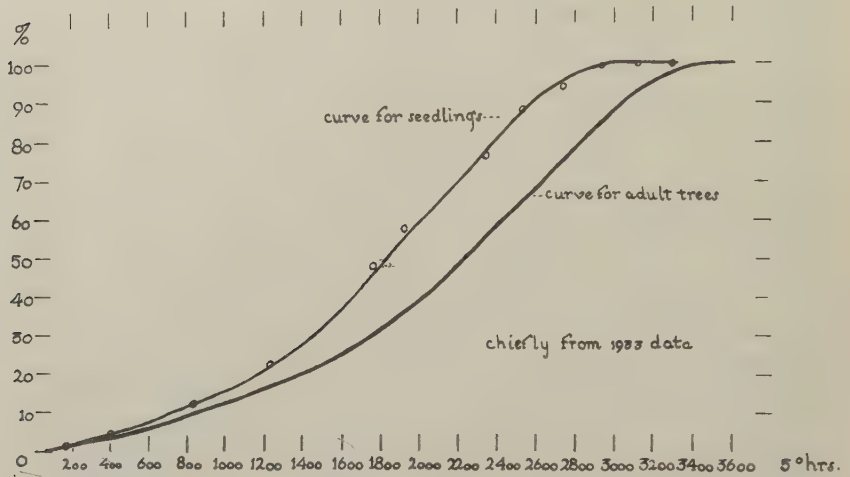


Fig. 3--Showing per cent of effectiveness of developmental units depending upon the amount of previous accumulation of five hours.

of cold, the changes must be gradual changes, and the effectiveness of conditions suitable for growth gradually increased.

The time when response to warmth first begins, or as it is called the phenological threshold of time, is another point in dispute. The old "temperature-summers" usually assumed that January first was the correct date. Gardner (24), 1929, thought that for pear shoots early February was the time. However, the results here presented show that there really is no date, but that the time depends upon the accumulation of temperatures that bring about after-ripening, and the time of year when developmental units become of sufficient value to be worth recording, depends very largely upon the weather during the year in question. December first was arbitrarily selected as the threshold of time

in order to be sure that all progress was included, but it is not thought that December first is the actual threshold of time for very many individuals even of the species studied. There is much greater variation in the time of leafing in plants brought in early in the season, and progressively less variation as the season advances, until the plants brought into the laboratory from outdoors in early April leaf very nearly together. This fact is taken as indicating that there is great variation among the elm plants in the time when after-ripening begins, but that the total 5°C . temperature that must be accumulated for the completion of after-ripening is very nearly the same.

The matter of physiological changes occurring in the buds as after-ripening progresses and time of leafing approaches does not come within the scope of this paper, though it is a matter of much interest and far-reaching possibilities.

It is concluded from the evidence obtained from these experiments that the breaking of dormancy is not due to freezing, but to the accumulation by the buds of a prolonged experience of temperatures around 5°C .; that this mass of accumulation reaches a point, usually sometime during December, where experience of warmth is effective at a much reduced rate; and that the accumulation of a mass of about 3,000 units of 5°C . is necessary before after-ripening is complete and accumulation of experience of conditions suitable for growth proceeds at a maximum rate.

Conditions and Factors that Bring About Leafing

It is obvious from the results presented above that warmth has much to do with bringing about leafing, though the effectiveness of different temperatures must be determined by experiment. Other factors suggested as possibly influential are: relative humidity, soil moisture, soil temperature, wetting by rain, day length, and light intensity. Shelford (56), 1926, and in a series of other papers has shown that relative humidity has a marked effect on time of emergence of insects from pupae, and it should therefore be examined as a factor in determining bud opening. Furthermore, an analysis of the situation would suggest that relative humidity does have an effect, because, since leafing is largely a matter of vacuolation and elongation of the internodal cells in the bud, any reduction in water loss would seem to assist in earliness of bud opening. The same line of reasoning would suggest that soil moisture and soil temperature might make considerable difference in time of leafing, for if water can more readily be absorbed by the roots it might be available for more rapid cell elongation in the buds. However, water loss from

winter buds is so slight and even the quantity of water necessary for bud opening is so much less than that lost in transpiration after the leaves are exposed, that the importance of water balance, as influenced by external factors during the interval before leafing begins, would seem to be slight.

A series of experiments were tried in which relative humidity, soil moisture, and wetting of the twigs were tried out as influencing time of bud opening. Potted seedlings were incubated at various temperatures with various relative humidities, but the variation in time of emergence under any one relative humidity always fell within or almost within the usual range of variation at each of the other relative humidities of the same temperature. That is, relative humidity seemed to have no effect, though it is possible that extremely low humidities might be retarding. Soil moisture, within any possible natural range for this climate, also failed to give any correlation. It was only with extreme drouth in the warmth of the greenhouse that retardation was noted. In the wetting experiments the seedlings which were never wetted during watering operations leafed slightly ahead of those wetted, on the average, but it was felt that the coldness of the water was a fully adequate explanation for the difference. Another indication that soil and air moisture are factors with slight if any effect on time of bud opening, is the complete lack of correlation found between number of rains and damp days and time of coming into leafing. It did not occur to the author to try the effect of different soil temperatures on leafing while the facilities were available to him at Chicago, but soil temperature was tried as a factor by Ikeda (34), 1932, with negative results. Further, the work of Denney and Stanton (16), 1928, in stimulating a single pair of lilac buds into activity without response on the part of the other buds of the plant, would indicate that the problem was a matter of external stimuli acting directly on the bud, rather than soil conditions acting on roots. The results of Howard (32), 1915, and Curtis (9), 1918, showing that the rest period is confined to the buds or to the buds and cambium would appear to bear out the idea that soil conditions are of minor importance in this connection.

The work of various investigators, as summarized by Gardner (25), 1921, on the effect of light on the germination of seeds, shows that light might well have an effect on the leafing of trees. Length of day experiments, also, suggest an effect of day-length on bud opening. To check these factors, the author carried potted seedlings and cut twigs at 20° C. and in the greenhouse under different lengths of day and in darkness. No effect of light nor length of day could be found. Some effect of

sunshine was noted, but when a correction was made for the increase in bud temperature due to sunshine, the indicated effect of bright light as such, disappeared.

It would appear, then, from as careful testing of factors as was found possible, that the only external factor having an influence on the time of leafing in white elm under normal conditions, is bud temperature. There is no doubt in the author's mind that internal physiology, due to experiences with conditions during the previous autumn and before, and due to hereditary constitution, has much to do with the influence of bud temperature. The observed fact that certain white elms in an avenue are always earlier or later in their leafing than are the majority of the individuals of the species would demonstrate beyond question that internal physiology has an effect.

Speed of Development at Different Temperatures

Leafing.- In an attempt to determine the speed of development of white elm toward leafing at different temperatures, a great series of potted seedlings and of cut twigs were incubated at many different constant temperatures. But the greater share of them proved to be of value only in giving better direction to later experiments. The cut twigs were never satisfactory except as they were used in the very last stages before opening, and all the first of the experiments had to be thrown out because of experimental errors that had not been taken into account. The chief trouble at first was that incubation was started too soon and the time of leafing of the poorly after-ripened seedlings varied too greatly to be of much value. Several other experiments were ruined by mechanical difficulties with equipment or more or less unconscious interference by other people.

The method that was ultimately worked out as satisfactory was to determine the relative speed of development during the latter part of the period before bud opening. The most successful experiment was carried on in 1933 starting on March 30 and running until April 13. Potted seedlings that had spent the winter outdoors in a corner protected from the sun were brought in in sufficient quantity to fill the 20° C. incubator and the 5° C. portion of the refrigerator. Those in 5° C. were brought in at the same time as the others to avoid progress under outdoor conditions, while the experiment was being carried on. After-ripening was known to be 99 per cent complete and a 1 per cent increase was made in the time records of those held for a week at 5° C. to bring the results into conformity with those from the plants put directly into 20° C. This unfortunate complication was made

necessary by lack of facilities for carrying on the tests at so many temperature levels in the time before the plants in 20° C. began to come into leaf. Successive batches of plants were put into the constant temperature incubator, set at different temperature levels, and left there for 20 hours, and then were returned to 20° C. Time was wasted in resetting the incubator, but this could not be avoided. The latter half of the experiment was carried on with the plants that had been held back in 5° C. The two lower temperature levels above 5° C. were supplied by the refrigerator after the stock plants were removed. Unfortunately temperatures between 9° C. and 18° C. were impossible to obtain with the equipment available. The results of this experiment are given in Table V. It is necessary to be very clear as to just what stage of development is meant by the expression "to leaf." Different investigators have applied the term to various stages of bud opening, but in the present author's use it means the time when the first green leaf pulls free from the bud mass. This is a definite incident of brief duration and its use as the end point has proved quite satisfactory.

The variation in the time to leafing under each set of conditions was less than 10 per cent between maximum and minimum. This is much less variation than was met with in the ordinary full time to be leafing experiments, and the means made a very good series. In determining relative speeds of development from these means, 20° C. was taken as the standard and 20 added to the recorded hours to leafing at that temperature, to make a total representing no progress whatever other than that while the plants were in 20° C. One hundred fourteen hours plus 20 hours gives 134 hours. The actual time to leafing was subtracted from this total of 134 in each case to find how much progress equivalent to that in 20° C. had occurred during the 20 hours in the other temperature (column 4). Then the total time it would have taken for leafing in each temperature was computed by first finding the per cent of efficiency of the other temperatures by dividing the amount of 20° progress shown in them (column 4) by 20, and then dividing the per cent so obtained into 134, which was the actual time to leafing in 20. These values (column 5) represent total elapsed time to leafing, but to get data for a curve of velocity of development, speed of progress rather than how long it takes, must be known. Since the reciprocal of the time elapsed is the speed, reciprocals were substituted for purposes of plotting (column 6), or their proportional equivalents in more easily handled denominations (column 7). Using these values in column

TABLE V

RELATIVE SPEEDS OF DEVELOPMENT IN WHITE ELM.
1933 EXPERIMENT

1.	2.	3.	4.	5.	6.	7.
Seed- ling Incubated 20 Hrs. at °C.	Total Mean Time in Hrs. to Leafing. All But 20 Hrs. at 20° C.	Time in Hrs. Saved Due to Progress at Other Temp. Than 20° C.	20 Hrs. at Other Temp. Equal to Hrs. at 20° C.	Under Constant Temp. at This Rate Leafing Would Be- gin in Hrs.	Recip- rocals of Time to Leafing	or
38	132.0	2.0	2.0	1140.0	.00088	0.9
37	129.4	4.6	4.6	495.7	.00202	2.0
35	124.0	10.0	10.0	228.0	.00441	4.4
32	117.0	17.0	17.0	134.1	.00746	7.5
30	114.0	20.0	20.0	114.0	.00877	8.8
28	112.2	21.8	21.8	104.6	.00958	9.6
25	110.4	23.6	23.6	97.5	.01056	10.3
22	111.8	22.2	22.2	111.8	.00982	9.8
20	114.0	20.0	20.0	114.0	.00877	8.8
18	117.4	16.4	16.4	139.0	.00719	7.2
9	133.1	0.9	0.9	2533.0	.00039	0.4
7	133.8	0.2	0.2	11400.0	.00009	0.1
5	134.0	0.0	0.0		0.0	0.0

7, a velocity curve was plotted (Figure 4).

For additional points on the velocity curve it was necessary to use the results of an experiment conducted at Chicago beginning in February, 1932, and of an experiment conducted at Oberlin in 1931, beginning at about the same time of year. The experiments were begun too early and show in each temperature a great variation in the time to leafing; a variation that is usual in the case of experiments begun before March. However, after slight corrections were made for degree of after-ripening, the averages of the two years make a good series and agree with those of the 1933 experiment much more closely than was expected.

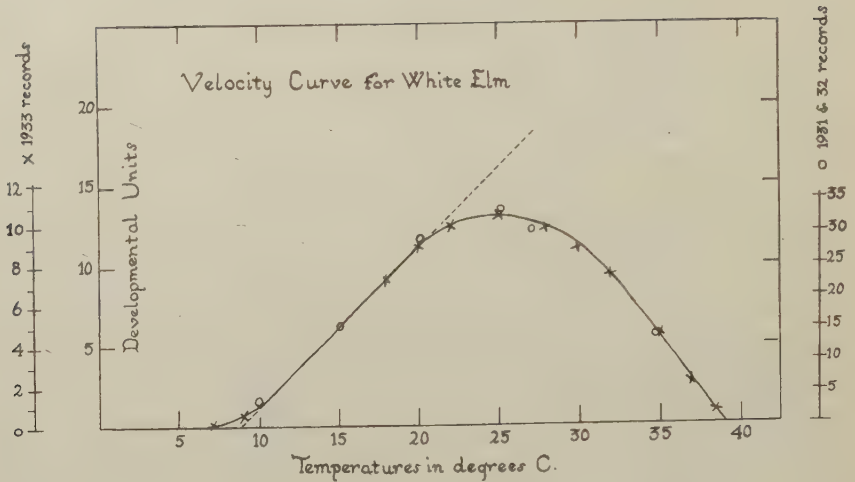


Fig. 4---The curve of the relative effectiveness of different temperatures in bringing about leafing in white elm.

Table VI gives the results of the 1931 and 1932 experiments. It should be noted that total elapsed time for 10° are in part computations. The plants at this temperature were still dormant a week before it was necessary to bring the experiment to a close. In order to obtain the best results possible, they were placed under 20° conditions until leafing occurred, and from the data so obtained, the total indicated time was computed.

These records, as well as those of Table V, were used in the plotting of Figure 4.

It is probably necessary to point out that the two experiments of 1931-1932 and of 1933 were performed after different amounts of progress had been accumulated outdoors, and after different degrees of after-ripening had occurred. Due to these differences, the total time to leafing at each temperature is unlike in the two years, and the reciprocals are necessarily different also. However, the relative speed, and not the distance travelled, is the important thing, and relative speed is what the reciprocals show. In using the data from the experiments of the two years for plotting a velocity of development curve, it was necessary to use different coordinates, as is shown in Figure 4. This was because the reciprocals were on different scales in the

TABLE VI

RELATIVE SPEEDS OF DEVELOPMENT IN WHITE ELM
1931 AND 1932 EXPERIMENTS

°C.	Time in Days Until Each Plant Began Leafing	Ave. Days to Leafing	Ave. Hrs. to Leafing	Recip- rocals	or
35	35, 34, 31, 30, 30, 29, 28, 28, 25	30	720	.00139	13.9
30	18, 17, 17, 16, 15, 15, 15, 14, 14, 14, 13, 11	15	360	.00278	27.8
27	19, 18, 16, 14, 14, 14, 13, 13, 12, 11	14	336	.00298	29.8
25	16, 16, 16, 14, 13, 13, 12, 12, 11, 10, 10	13	310	.00323	32.3
20	20, 18, 16, 16, 15, 15, 15, 14, 13, 13	15	360	.00278	27.8
15	31, 30, 29, 26, 26, 25	28	672	.00149	14.9
10	150, 145, 140, 100	126	3024	.00033	3.3
8	Very slight progress			---	---

two cases, although they were proportional among themselves.

From the velocity curve in Figure 4, a table was obtained of the indicated efficiency of each temperature on the scale (Table VII).

It may be readily seen from Figure 4 or Table VII that it is only between 11° and 20° that the effectiveness at each temperature is one unit more than that at the degree of temperature immediately below it. This portion of the scale is what Shelford (58), 1930, refers to as the medial temperature. If this descending proportion were maintained, 9° would be zero, although the actual zero point, or threshold, appears to be 6°. The effectiveness of the temperatures from 7° through 10° is greater than would be expected if the progress under different temperatures were

directly proportional, and it is necessary for summation purposes, therefore, to correct their values to make them proportionate. In the same way, the temperatures above 20° are proportionally less effective than the increase in the temperature would indicate, and

TABLE VII

WHITE ELM DEVELOPMENTAL UNITS AT DIFFERENT TEMPERATURES
FROM THE VELOCITY CURVE (FIG. 4)

°C	DU	°C	DU	°C	DU	°C	DU
39	0.0	29	11.5	19	10.0	9	0.5
38	1.1	28	12.0	18	9.0	8	0.2
37	2.5	27	12.4	17	8.0	7	0.1
36	4.0	26	12.8	16	7.0	6	0.0
35	5.4	25	13.0	15	6.0	5	0.0
34	6.7	24	12.8	14	5.0		
33	8.0	23	12.5	13	4.0		
32	9.3	22	12.2	12	3.0		
31	10.3	21	11.8	11	2.0		
30	11.0	20	11.0	10	1.2		

above 25° are actually less effective than are temperatures lower on the scale. These also must be given corrected values to bring their indicated effectiveness into proportion with the medial range. The effectiveness of 36° is not 36 units nor even, subtracting 9° as the threshold, 27 units. The amount of progress that a bud accumulates during an hour at 36° is only as much as is accumulated at 13°, and since that value on the proportional scale is 4, the value of 36° is recorded as 4 units. By using the values given in Table VII, the hour by hour temperatures, as given on thermograph records, were corrected to represent the actual progress toward leafing during each hour. The resulting developmental units were added up to represent the progress for the day. This matter will be discussed at greater length in the section on Application to Phenological Records.

The author is perfectly well aware of the fact that this velocity curve is based on the results of the reactions of too few plants. To be sure, the records listed are only a small proportion of the records obtained, and no records that appeared to have any dependability disagreed very markedly with the results

here given. But even the complete mass of material experimented with was too small to yield entirely dependable results. The author can but plead that all was done that could be done and that further time was not allowed him. The fact that the plotted points come into close conformity with each other in the formation of a curve does not prove that the resulting curve is without considerable error.

In its shape, this curve--the curve of the efficiency of different temperatures in inducing progress toward leafing in white elm--is not quite what was expected. At the end toward the zero, the straight line limits are reached a number of degrees sooner than is usual in such curves, the apex is unusually broad, and the descending arc is convex instead of the usual concave. However, this is not a curve of the velocity of growth, but the curve of the accumulation of the experience of good conditions necessary before growth begins. It may be that in its velocity of growth curve, the white elm conforms much more closely with the usual curve. Pack (49), 1921, found that *Juniperus* seeds will not germinate except at temperatures about 5° C., but that the seedlings grew best at about 15° C. The fact of a certain type of reaction to temperature by an organism during one vital process, is no proof that its reaction during another vital process will be similar.

Flowering.-- Many experiments were tried on white elm in an effort to determine the speed of development toward flowering. It was necessary to use cut twigs for this purpose, and they soon proved unsatisfactory. It was never possible to determine the entire time to flowering in any constant temperature, because twigs cut in January flowered very imperfectly if at all. The only method yielding results of any value was similar to the method found most successful with leafing. Twigs were cut when the flower buds first showed definite swelling, and incubated at the different temperatures until the first pollen was released from the stamens. This time of the first release of pollen was the time always taken as the beginning of flowering. In the selection of the twigs to cut for this experiment, care was taken that they should all show the same degree of scale separation.

The data obtained from even this best method was rather uneven and conflicting. The author feels that more and better data is imperative before a velocity curve can be drawn. All that can definitely be stated is that as far as could be determined the relative efficiencies of different temperatures are much the same for flowering as for leafing. The total accumulated mass of effective temperature for flowering is much less than for leafing, however. And the data suggests that after-ripening is further

advanced at the same date in the flower buds than in the leaf buds.

The Thermoconstant

The thermoconstant is the sum total of accumulated developmental units that is necessary before the vital process in question can be completed. The thermoconstant of the leafing of white elm seedlings may be determined with accuracy from the data here presented, if corrections are made for the effects of after-ripening. The indicated totals for plants brought indoors early in the winter are far higher than those for plants brought in later, but as is illustrated earlier in this paper, the difference is in proportion to the amount of after-ripening the plants had experienced. The experiments in which the need of application of the corrections for after-ripening was avoided, gave very similar results. In both the case of the plants left for two months in 5° and in this way completely after-ripened, and in the case of those shocked with ether during late March, leafing occurred in 20° C. at an average of about 5.7 days. The developmental unit value of 20° C. has been found to be 11, and therefore the thermoconstant is 1505 DU.

This thermoconstant of about 1500 DU appears very near the truth for the seedlings, but there is abundant evidence that the thermoconstant for leafing in the adult trees is a considerably larger figure. Even during warm weather the adult trees do not begin to come into leaf until nearly a week after the seedlings do, and further, there is plenty of evidence from a study of weather records and time of leafing that the thermoconstant for the adult trees must be over 2000 DU.

From the experimental data no indication can be found as to the thermoconstant for flowering in white elm. All that is sure is that the total must be much smaller than the total for leafing. The determination of its approximate value must wait until the experimental data is applied to phenological records.

We may conclude, then, that the thermoconstant for leafing in white elm seedlings is about 1500 DU, that the thermoconstant for the leafing of adult trees of this species is considerably more than 1500 DU, and that the thermoconstant of flowering is considerably less than 1500 DU.

CORRELATION OF EXPERIMENTAL RESULTS WITH PHENOLOGICAL DATA

The experimental approach, as attempted in this paper, is only one way of getting at the problem of why trees blossom and leaf at the time they do. The more usual attack on the problem is to record the dates of the actual happenings, and to collect data on the weather, and then to try to correlate the two. Or, more often still, the data is collected merely as a pleasant spring pastime, made more interesting by the variation in the dates that occurs from year to year. This variation is greater than is generally supposed. At Oberlin from 1930 to 1935 the date of flowering of white elm varied from April 20 to May 13. Thomas Mikesell collected records in Wauseon, Ohio, for 24 years as published by Smith (62), 1915, and he found the variation for this species to be from March 30 to April 24 for flowering and April 24 to May 18 for leafing. There can be little doubt that the reason for this variation is a corresponding variation in accumulated warmth. It would be simple and quite satisfactory if the relation were a direct one without complications. On the assumption that it is so, many different people have advanced the theory that the sum of positive mean temperatures from January first until the phenological happening, is always the same for all years. Lamb (58), 1915, cites Brendel (7), 1887, to this effect, apparently without having checked his own data. This assumption is still held by many, in spite of the fact that it has been proved false over and over again. Seeley (55), 1917, worked with the Mikesell data and found that the sums of the positive mean daily temperatures for peach disagreed 78 per cent. For this same data, a computation of the sums to leafing in white elm gives totals ranging from 317.4 to 566.2, not counting the total of 703.8 for 1894 which must represent an error. Similar sums from Oberlin data for only five years range from 338.8 to 569.0. With such variations as these, prediction is quite impossible, and it would seem to be demonstrated that the effect of warmth is different from that assumed.

The data obtained from the experiment discussed in this paper, ought to explain this variation in the outdoor records better than anything that has been tried hitherto. And the author feels that his conclusions should stand or fall on the basis of success or failure in their application to this

phenological problem.

The application of the experimental data to the phenological records, however, involved many difficulties and an enormous amount of labor. If it were possible to take the mean temperatures for the various days and assign developmental unit equivalents to them for summations of the thermoconstants, the problem would be simple, but this is not possible and the problem is anything but simple. There appear to be three main reasons why daily averages have no meaning in this work: (1) the speed of development at different temperatures is proportional through only about one-third of its range; (2) hourly temperatures above the threshold are effective even though the average for the day is below the threshold; and (3) temperatures at the higher ranges are less effective than much lower temperatures. It is necessary to consider the effectiveness of temperature hour by hour for each day; Shelford (57), 1929, has demonstrated this necessity repeatedly. But even after these demands are met, there are two more complications. One is the need of correcting for the degree of after-ripening, as is discussed in the section on that subject, and the other is the need for correction for the effect of sunshine.

Correction for the Heating Effect of Sunshine

The early attempts to apply the experimental results to interpretation of the outdoor records gave very different thermoconstants for the different years. The first assumption was that rain or dampness might increase the efficiency of temperature, but corrections made on this basis yielded even more discordant results. Clearly the sunshiny days were usually days of greater than expected progress, and since experiment had shown no effect of light as such, a heating effect by sunshine was indicated.

Search through the literature revealed a considerable amount of work done on the question of the heating effect of sunshine on plant tissues. Whitton (67), 1897, noticed that whitewashed buds of peach swelled much less than unwhitewashed buds, were less subject to damage by cold, and flowered one to six days later. In 1900 (68), he measured bud temperatures and found that in bright sunlight the whitewashed buds were sometimes 15° C. cooler than the buds that had been left their natural color. Welden (66), 1926, felt that in all probability the reason why peach trees in Southern California leafed so poorly in the years 1904, 1924, and 1926 was that the winters were too mild and the amount of sunshiny weather too great. This explanation was suggested by the fact that the trees in fullest sun leafed most poorly, and as a control measure he advocated shading by wind

breaks. Wiegand (69), 1906, assembled the bud scales of a horse chestnut bud about the bulb of a mercury thermometer, and found that the temperature in bright sunlight increased up to 8.3° C. within half an hour. His observation was that time of bud swelling is correlated with bud color, and that blackening poplar buds caused earlier opening. There is little doubt that sunshine does make a difference in bud temperature and in time of bud opening.

The author felt that, before correlation of experimental results with phenological data could be done with any hope of significant results, a system of correction for the effects of sunlight must be obtained. This system of corrections would certainly be only approximate, at best, because completely satisfactory results could be expected only from a continuous record of the temperature of the bud itself. But even for approximately accurate corrections the actual temperature of elm buds must be determined under a great variety of conditions. Degree of cloudiness, time of day and wind velocity all might be expected to influence bud temperature. However, mercury thermometers are hardly usable in objects as small as elm buds, and so it is necessary first to work out the problem of the most suitable apparatus for this purpose.

The various investigators in the field have used instruments of two main types. Ursprung (65), 1903-1904, and Seeley (55), 1917, as well as Wiegand (69), 1906, used mercury thermometers, whereas Stahl (63), 1896, Matthaei (46), 1905, Ehlers (21), 1915, and Shreve (60), 1919, all used thermocouples in some combination or other. The method decided on as most suitable for the investigation of the temperature of white elm buds, was that used by Shreve. A thermocouple of fine wires of copper and constantan was used in conjunction with a galvanometer provided with a damping key. A stand was constructed on a camera tripod to hold the galvanometer and to supply suitable protection and shade for one junction of the thermocouple. To reduce error as much as possible, the calibration of the apparatus was done by direct experiment, instead of by computation from only a few measurements. Water baths of various combinations of temperatures were used for calibration purposes, and the temperature of the water determined by accurate mercury thermometers. The deflection of the galvanometer needle was recorded and a chart of deflection was made to show the differences of temperature at the two junctions under different air temperatures. As an added precaution the attachments of the thermocouple to the galvanometer were always made at the ends of the wires, in order to reduce errors due to varying resistance of the wires.

With this apparatus a great many records, under various conditions, were taken, showing how much the temperature of the elm buds differed from the temperature of the air. To make the records, one junction of the thermocouple was thrust completely into the bud, the other junction was kept in well ventilated shade, and the deflection of the galvanometer needle observed. To determine the air temperature during each record, an accurate mercury thermometer was secured on the stand with its bulb in close proximity to the shade junction of the thermocouple.

By this method, the buds were found to respond very rapidly to differences in sunlight and wind. The sudden shading of a bud that was in full sunshine would cause its temperature to fall approximately to air temperature in a very few minutes. But this quick response with its marked rises and sudden drops under only slightly varying external conditions, made any accurate prediction of the temperature of a bud very uncertain. However, general averages were obtained which proved to be reasonably consistent, and from these general averages smoothed curves were constructed and from the smoothed curves, Table VIII was arranged. This table is thought to be reasonably correct for white elm in a statistical sense. The temperature of the bud would not be found to be that in the table at most of the times it is measured, but the average would probably be close to that shown.

As Table VIII shows, a strong wind was found to reduce the effectiveness of sunlight to approximately that under partly cloudy conditions. The heating effect of full sunlight in still air was greater than that shown for full sunlight and moderate wind, but still air occurs so rarely that it is hardly worth including. The sudden drop in heating effect shown for May first is due to the fact that by that time the buds have swollen sufficiently to expose much of the green portion of the scales. This actual date may be as early as April 15 instead of May 1, and adjustments must be made for the year under consideration. Evidence that correction for sunlight is worth while is supplied by computation of corrected and uncorrected thermoconstants under outdoor conditions. The thermoconstant for outdoor potted seedlings in 1933 was 1494 DU when corrections are made for sunshine, and only 1050 DU when corrections are not made for sunlight. The 1494 DU thermoconstant in sunlight is very close to the total obtained from experiments, and the uncorrected thermoconstant of 1050 DU is much too low. Figure 5 is the temperature curve of a warm mostly clear day showing something of the relation between air temperature, bud temperature and effective temperature. In the case of days as warm as this, sunshine considerably reduces the amount of progress. In cold days the opposite is true. If a day

TABLE VIII
APPROXIMATE INCREASE IN DEGREES CENTIGRADE IN WHITE ELM BUD
TEMPERATURE DUE TO SUNSHINE

	8 & 4 o'clock			9 & 3 o'clock			10 & 2 o'clock			11 & 1 o'clock			12 Noon		
	0,m	0,s	0,m	0,m	0,s	0,m	0,m	0,s	0,m	0,m	0,s	0,m	0,m	0,s	0,s
Jan. 15	0.5	0.0	0.0	2.0	1.0	0.0	3.0	2.0	0.5	4.0	2.5	1.0	4.5	3.0	1.5
Feb. 1	0.7	0.2	0.0	2.5	1.2	0.2	3.5	2.5	0.7	4.4	2.9	1.2	4.8	3.2	1.7
Feb. 14	1.0	0.5	0.0	3.0	1.5	0.5	4.0	3.0	1.0	4.8	3.3	1.5	5.2	3.5	2.0
Mar. 1	1.1	0.6	0.1	3.3	1.8	0.7	4.4	3.3	1.4	5.1	3.7	1.7	5.6	3.8	2.3
Mar. 15	1.2	0.7	0.2	3.7	2.2	1.0	4.7	3.7	1.7	5.5	4.0	2.2	6.0	4.2	2.7
Apr. 1	1.4	0.9	0.4	4.1	2.6	1.5	5.1	4.1	2.1	5.9	4.4	2.6	6.4	4.6	3.1
Apr. 15	1.5	1.0	0.5	4.5	3.0	2.0	5.5	4.5	2.5	6.3	4.8	3.0	6.7	5.0	3.5
May 1	1.0	0.5	0.0	3.5	2.0	1.0	4.5	3.0	1.5	4.8	3.3	1.5	5.0	3.5	2.0

0 = full sunshine m = moderate wind
0 = partly cloudy s = strong wind

April 6, 1929 at Oberlin, Ohio.

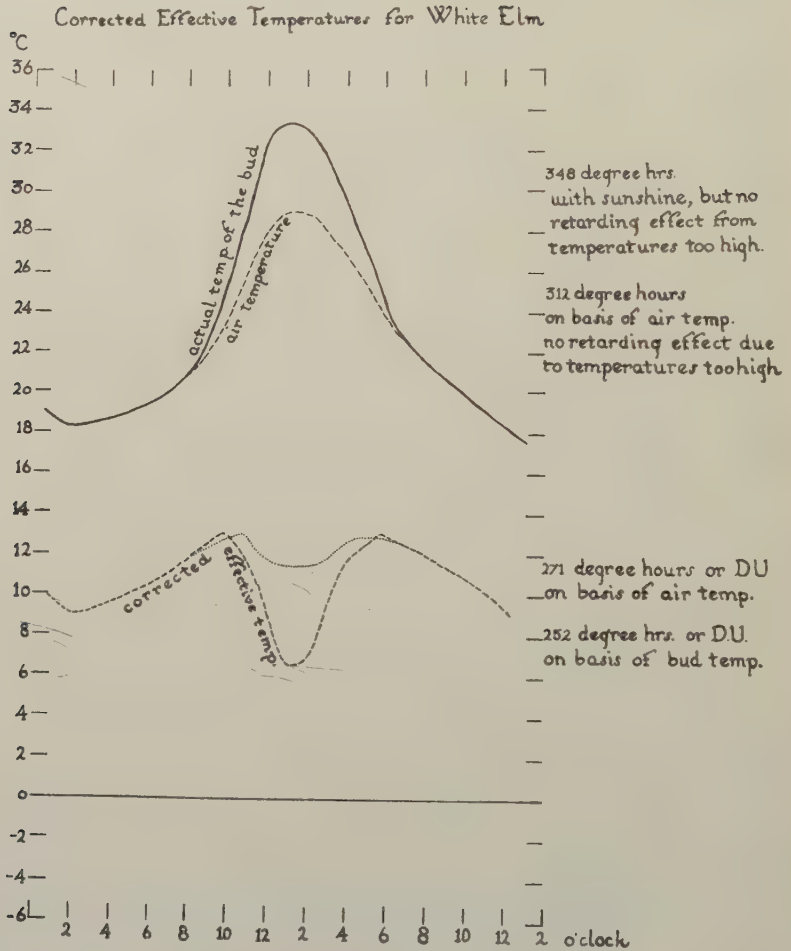


Fig. 5--The smoothed temperature curve of a single day.

of very much this type of temperature curve but with an average temperature of 6.8° were taken for comparison, it would show an average bud temperature of 8.5° and an actual effectiveness of 50.1 DU instead of 21.8 DU that the air temperature alone would make possible.

Computation of Daily Developmental Unit Totals

The method of computation found necessary, in order to obtain reliable results, was to make tables of the hour-by-hour air temperatures, correct for the effect of sunlight and then assign its developmental unit equivalent to each hour. The totals for days so arrived at seemed to be reliable. Table IX gives two sample days showing the method. This method is the one long used by Shelford (57, p. 194) and is modified only by the addition of correction for sunlight.

TABLE IX

SAMPLE DAYS SHOWING HOW DEVELOPMENTAL UNIT TOTALS
ARE OBTAINED FROM THERMOGRAPH RECORDS

April 21, 1933				April 29, 1933			
Hr. of Day	Air Temp. C	Bud Temp. C	DU	Hr. of Day	Air Temp. C	Bud Temp. C	DU
6 A.M.	5.6	5.6	0.0	6 A.M.	8.9	8.9	0.5
7	7.2	7.7	0.2	7	11.1	11.4	2.4
8	8.9	10.4	1.5	8	16.1	16.6	7.6
9	10.6	15.1	6.1	9	20.6	23.8	12.5
10	12.2	17.7	8.7	10	23.9	28.1	11.8
11	13.9	20.2	11.2	11	26.1	30.7	10.4
12 Noon	15.6	22.3	12.4	12 Noon	27.1	31.8	9.4
1	16.7	23.0	12.6	1	29.4	34.0	6.7
2	17.8	23.3	12.7	2	30.0	34.2	6.4
3	15.6	20.1	11.1	3	30.6	33.8	6.9
4	12.2	13.7	4.7	4	30.0	30.8	10.3
5	9.4	9.9	1.2	5	28.3	28.5	11.6
6	7.2	7.2	0.1	6	27.1	27.1	12.5
7	5.6	5.6	0.0	7	24.4	24.4	12.9
8	4.4	4.4	0.0	8	21.1	21.1	11.9
9	3.9	3.9	0.0	9	18.3	18.3	9.3
10	3.3	3.3	0.0	10	17.2	17.2	8.2
11	2.8	2.8	0.0	11	16.1	16.1	7.1
12	2.2	2.2	0.0	12	15.0	15.0	6.0
1	1.7	1.7	0.0	1	14.4	14.4	5.4
2	1.7	1.7	0.0	2	13.9	13.9	4.9
3	1.1	1.1	0.0	3	14.4	14.4	5.4
4	0.6	0.6	0.0	4	14.4	14.4	5.4
5	0.6	0.6	0.0	5	13.9	13.9	4.9
Developmental units for the day			82.5	Developmental units for the day			190.4

The determination of the daily developmental unit totals by means of the method illustrated in Table IX is quite a simple matter (though very time consuming), if a thermograph or any other constant temperature record is available. However, constant temperatures are not often taken in connection with phenology records. Instead, as a rule, the only temperatures given are maximum and minimum with perhaps one other reading. Shelford (57, p. 198) gives Strachey's formula for computation of developmental units from maximum-minimum temperature records, though he considers it a poor substitute for computation from hour-by-hour data. Strachey's formula was tried in working over the Wauseon material, but comparison of the totals obtained by using it, with the totals obtained from thermograph records, proved disappointing. The main reason for its failure was that it did not and was not intended to provide for the heating effect of sunshine. The method finally used where thermograph records were not available was to draw curves of the hourly temperatures as indicated by the points reported and then to proceed as if the curve drawn were an actual thermograph record. After a good deal of practice and study of the shape of the daily temperature curve, it was found that on the average the developmental unit totals from the drawn curves agreed quite closely with the totals as obtained from thermograph records. Table X shows the comparative results with the three methods. The reader is assured that the curves were drawn from maximum-minimum thermometer readings and without reference to the thermograph records. The results are representative of a much longer series.

It may properly be objected that the use of the drawn curve introduces errors. It undoubtedly does, but it seems to be more accurate than any other method, known to the author, for computing totals from maximum-minimum temperature data. At the same time, one should never fall into the error of thinking of the constant temperature record as representing the temperature of the plant buds throughout the day. A thermograph can do no more than record the temperatures where it is, and as a rule the instrument is not placed in the crown of the tree. The author greatly regrets the necessity of the introduction of another source of error where there are already far too many, but if computation of thermoconstants from the data available is to be done at all, introduction of this source of error cannot be avoided.

Using the methods above described, the author went through five years of the Oberlin records and determined the corrected developmental unit thermoconstants for both leafing and flowering in white elm. The hour-by-hour developmental unit values were determined, as modified by the effect of sunshine, and then the

developmental unit total for the day was corrected for the effect of the degree of after-ripening (see p. 22). Thermograph records were available for the years 1931, 1933, and 1934. For 1930 and 1935, the only data to be had was a record of the weather, and

TABLE X

COMPARISON OF THE RESULTS OF COMPUTATION OF DEVELOPMENTAL UNIT TOTALS FROM A THERMOGRAPH RECORD, BY THE APPLICATION OF STRACHEY'S FORMULA, AND BY REFERENCE TO A CURVE DRAWN FROM MAXIMUM-MINIMUM THERMOMETER READINGS

Date 1933	Weather	Min. °C	Max. °C	10:00 P.M. °C	Ave. °C	Hr. by Hr. from Thermogr.	Strachey's Formula	Drawn Curve
Feb. 22	0	-6.1	15.0	8.3	6.1	62.5	73.0	62.1
23	0	1.7	11.1	2.8	5.5	25.5	31.1	28.6
24	0	-0.6	11.1	5.0	4.5	30.9	48.5	33.1
25	0	2.8	10.6	-1.1	5.0	7.8	3.4	8.0
Mar. 6	0	-8.3 -0.6	10.6	3.3	1.0	15.2	23.5	19.9
12	0	-6.7	11.1	5.6	2.6	24.7	50.4	31.5
13	0	4.4 6.1	10.6	7.8	8.5	21.6	8.2	10.9
DU Totals						188.2	238.1	194.1

temperatures for the maximum and minimum and for 10:00 P.M. for each day. Tables XI, XII, XIII, XIV, and XV give the data and results for these five years.

Besides these five years of the record for Oberlin, the very extensive records for Wauseon, Ohio (Smith (62)), were worked over also. Twenty-four years of these records for white elm have been completed up to the point of correction for the degree of after-ripening. Time will not allow this extensive operation, and the data from this source cannot be included here. This is especially to be regretted, because all the indications are that this final correction will bring the Wauseon results into close agreement with the thermoconstants obtained for the five Oberlin years.

TABLE XI
WEATHER AND DEVELOPMENTAL UNITS FOR WHITE ELM
OBERLIN, OHIO

Date	Weather	Temperature in C			DU	Daily 5 Hours	Leafing		Flowering	
		Min. 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.			Accum. 5 Hours	Cor-rected DU	Accum. 5 Hours	Cor-rected DU
1930 Dec. 5	0	-5.0	10.6	3.3	40.0	...	40	0.0	600	2.4
6	0	2.2	13.9	3.3	43.0	...	80	0.3	640	2.8
12	R	-1.1	12.2	12.2	56.0	...	300	1.7	860	4.8
13	R	11.7 2.2	17.2	9.4	130.0	...	320	3.9	880	11.4
17	R	1.1 -1.1	12.8	2.8	31.0	...	500	1.5	1060	4.0
1931 Jan. 1	0	2.8	12.8	12.2	54.0	22	680	4.3	1240	9.2
2	R	12.2	2.2	0.5	12.7	36	716	1.0	1276	2.3
3	S	-1.7	2.2	-3.3	0.0	13	729	...	1289	...
4	0	-9.4	0.0	-3.3	0.0	7	736	...	1296	...
5	0	-5.0	7.2	4.4	9.8	73	809	0.9	1369	1.9
6	0	4.4	12.8	12.8	49.6	25	834	5.0	1394	9.9
7	R	8.9	12.2	3.3	31.2	40	874	3.1	1434	6.6
8	R	1.1	5.6	0.0	0.0	45	919	...	1479	...
9	R	-1.7	0.0	-1.1	0.0	0	919	...	...	...
10	R	-5.0	-1.1	-6.7	0.0	0	919	...	...	...
11	R	-7.8	2.2	0.6	0.0	14	933	...	1489	...
12	R	0.6	7.2	2.8	0.0	67	1000	...	1556	...
13	R	0.6	5.0	5.0	0.0	98	1098	...	1654	...
14	R	5.0 -3.3	15.0	5.6	50.1	44	1142	7.5	1694	14.0

TABLE XI (CONTINUED)

Date	Weather	Temperature in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Ave.			Accum. 5 Hours	Corrected DU	Accum. 5 Hours	Corrected DU
1931 Jan. 27	R	-7.2	1.7	-0.6	-2.7	0.0	3	1145	...	1697	...
28		-2.2	1.7	-10.0	-3.1	0.0	20	1165	...	1717	...
		-17.2									
30		-17.8	-3.3	-5.0	-9.4	0.0	0	1165	...	1717	...
31	R	-6.7	-2.2	-8.3	-5.6	0.0	0	1165	...	1717	...
Feb. 1	R	-8.3	2.8	1.7	-2.3	0.0	22	1187	...	1739	...
2	R	-0.6	3.3	2.2	1.7	0.0	41	1228	...	1780	...
3		1.7	5.6	0.6	2.5	0.0	45	1273	...	1825	...
4		-0.6	5.0	-1.1	1.1	0.0	29	1302	...	1854	...
5		-3.3	1.1	-5.0	-2.2	0.0	1	1303	...	1855	...
6	R	-7.8	2.2	1.1	-1.9	0.0	13	1316	...	1868	...
7		-0.6	0.6	-5.6	-1.4	0.0	0	1316	...	1868	...
8	R	-7.2	1.1	-6.1	-4.3	0.0	1	1317	...	1869	...
9		-6.7	4.4	-0.6	-1.7	0.0	22	1339	...	1891	...
11		-3.9	3.3	0.0	-2.4	0.0	24	1363	...	1915	...
12	R	-1.1	7.8	7.2	3.9	0.0	70	1433	...	1985	...
13		0.0	6.7	-2.8	2.2	0.0	40	1473	...	2025	...
14		-5.0	-1.7	-3.9	-3.4	0.0	0	1473	...	2025	...
17		-6.7	3.3	1.7	-1.3	0.0	32	1505	...	2057	...
18		1.7	13.9	5.0	6.7	64.1	67	1572	15.4	2124	23.2
19		4.4	17.8	12.8	10.7	118.0	17	1589	29.5	2141	53.1
20		10.0	19.4	8.9	12.8	129.0	29	1618	32.2	2170	60.0
21		5.6	21.1	8.9	11.4	112.1	45	1663	30.3	2215	54.9
22		6.1	21.1	12.8	12.7	120.0	12	1675	32.4	2227	56.8
23	R	6.7	18.3	5.0	10.4	107.0	57	1732	31.0	2284	55.6

TABLE XI (CONTINUED)

Date	Weather	Temperature in C			DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. 1:30 P.M.	10:00 P.M.			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1931										
Mar. 25	R	-0.6	7.2	1.1	0.0	40	2632	...		
26	•	-5.0	0.6	-2.8	0.0	0	2632	...		
27	•	-3.9	1.1	-1.7	0.0	2	2634	...		
28	•	-2.8	3.9	-1.1	0.5	25	2659	...		
29	•	-2.8	7.8	0.0	2.5	35	2694	1.4		
30	C	-2.8	8.3	-0.6	2.9	35	2729	0.7		
31	•	-2.2	10.6	5.6	5.9	70	2799	16.5		
Apr. 1	R	4.4	12.2	1.7	6.6	20	2819	29.0		
2	•	-3.3	15.0	1.7	6.4	20	2839	46.0		
3	•	-1.1	15.6	3.3	7.3	30	2869	55.4		
4	•	-1.1	15.6	4.4	7.8	38	2907	65.3		
5	•	1.1	20.0	12.2	12.6	20	2927	114.2		
6	•	9.4	17.2	7.2	11.4	25	2952	106.1		
7	•	1.7	0.0	1.7	0.8	10	2962	0.0		
8	C	0.0	6.7	1.1	2.4	42	3004	1.7		
9	•	-3.9	15.6	4.4	7.5	50	3054	73.4		
10	•	2.8	22.2	17.8	16.0	10	3064	162.7		
11	•	16.7	31.1	17.2	21.9	0	3064	196.7		
12	•	6.7	21.1	12.2	17.1	10	3074	137.7		
13	•	9.4	25.6	11.7	16.9	1	3075	174.1		
14	•	7.2	11.1	3.9	7.6	50	3125	41.6		
15	R	1.1	7.8	3.3	4.9	60	3185	0.0		
16	R	2.8	10.0	10.0	8.2	10	3195	15.0		
17	R	10.0	25.6	16.1	18.9	0	3195	193.1		
18	R	14.4	21.7	8.3	15.4	20	3215	169.0		
19	•	3.9	17.2	6.1	10.6	40	3255	107.3		
Leaf 20	•	3.9	19.4	8.3	53.5	10	3265	51.4		
Totals					3907.4			2379.0		862.4

TABLE XII
WEATHER AND DEVELOPMENTAL UNITS FOR WHITE ELM
OBERLIN, OHIO

Date	Weather	Temperature in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Ave.			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1930											
Dec. 9	☉	0.6	10.0	3.3	5.6	35.0	...	220	0.8	780	2.7
10	☉	1.7	11.1	7.2	7.1	45.0	...	250	1.1	810	3.6
11	R ☉	4.4	10.0	6.1	6.4	35.0	...	290	0.9	850	3.0
		1.1									
1931											
Jan. 2	☉	-8.9	0.0	0.0	-2.5	0.0	5	1010	...	1570	...
3	☉	-1.1	4.4	0.0	1.1	0.0	35	1045	...	1605	...
4	R ☉	-2.8	5.6	3.3	2.9	0.1	60	1105	...	1665	0.0
5	R ☉	3.3	3.3	0.6	2.2	0.0	35	1140	...	1700	...
7	☉	-11.7	1.7	-8.3	-4.6	0.0	15	1155	...	1715	...
8	☉	-10.0	-1.1	-7.2	-4.8	0.0	5	1160	...	1720	...
10	☉	-7.2	1.7	-1.7	-1.9	0.0	10	1170	...	1730	...
11	☉	-3.9	4.4	0.0	1.2	0.0	35	1205	...	1765	...
12	S ☉	0.0	3.3	-2.2	1.1	0.0	20	1225	...	1785	...
16	R ☉	-2.2	4.4	0.0	0.4	0.0	35	1260	...	1820	...
17	☉	-5.0	4.4	-1.1	0.0	0.0	30	1290	...	1850	...
18	R ☉	-3.9	2.2	2.2	-0.3	0.0	15	1305	...	1865	...
19	S ☉	-1.7	6.1	-1.1	1.7	0.0	40	1345	...	1905	...
20	S ☉	-3.9	1.1	-9.4	-2.9	0.0	5	1350	...	1910	...
22	☉	-10.0	-0.6	-3.9	-4.7	0.0	0	1350	...	1910	...
23	☉	-8.3	1.7	-1.1	-1.6	0.0	10	1360	...	1920	...
24	☉	-1.7	8.9	5.0	5.0	22.1	70	1430	...	1990	8.5
25	☉	3.9	10.0	3.3	5.5	8.9	50	1480	4.6	2040	3.6
26	☉	-1.7	8.9	0.6	4.0	19.7	35	1515	4.3	2075	8.3

TABLE XII (CONTINUED)

Date	Weather	Temperature in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. 1:30 P.M.	10:00 P.M.	Ave.			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1931											
Jan. 27	0	0.0	7.2	0.6	2.9	1.2	40	1555	0.3	2115	0.5
28	0	-2.8	0.6	0.6	-0.4	0.0	0	1555	...	2115	...
29	0	0.0	2.2	-2.8	-0.3	0.0	15	1570	...	2130	...
30	S	-3.3	10.0	2.8	3.1	1.4	40	1610	0.3	2170	0.7
31	0	-4.4	-1.1	-2.8	-3.2	0.0	0	1610	...	...	...
Feb. 1	C	-6.1	1.7	1.1	-1.1	0.0	10	1620	...	2180	...
2	0	-1.7	2.2	-3.9	-1.0	0.0	10	1630	...	2190	...
3	0	-6.7	7.2	5.6	0.5	6.2	50	1680	1.5	2240	3.1
4	C	-5.6	0.0	-6.1	-3.2	0.0	5	1685	...	2245	...
5	0	7.2	3.3	1.1	-1.0	0.0	25	1710	...	2270	...
6	C	-3.3	5.6	-2.2	1.4	0.0	25	1735	...	2295	...
7	R	-2.2	6.7	0.6	2.9	0.0	40	1775	...	2335	...
8	0	0.6	6.7	0.0	3.2	2.0	40	1815	0.6	2375	1.1
9	0	-1.1	4.4	-1.1	0.0	0.0	30	1845	...	2405	...
10	0	-7.8	0.6	-7.2	-4.0	0.0	5	1850	...	2410	...
11	S	-8.9	2.2	-0.6	-1.0	0.0	10	1860	...	2420	...
12	0	-0.6	5.6	3.9	3.2	0.0	70	1930	...	2490	...
13	R	2.2	5.0	-5.0	0.6	0.0	35	1965	...	2525	...
14	0	-10.0	-4.4	-6.1	-6.5	0.0	0	1965	...	2525	...
15	0	-7.2	5.6	1.1	1.0	3.1	35	2000	1.2	2560	2.0
16	R	0.0	7.2	1.1	3.9	0.0	40	2046	...	2600	...
17	R	1.1	6.1	0.6	3.2	0.0	40	2080	...	2640	...
18	R	-0.6	1.1	0.0	0.3	0.0	5	2085	...	2645	...
19	S	-0.6	1.7	0.0	0.5	0.0	10	2095	...	2655	...
20	S	-0.6	1.7	0.6	0.4	0.0	10	2105	...	2665	...

TABLE XII (CONTINUED)

Date	Weather	Temperature in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Ave.			Accum. 5 Hours	Corrected DU	Accum. 5 Hours	Corrected DU
1931											
Feb. 21	S	-1.1	0.0	0.0	-0.4	0.0	0	2105	...	2665	...
22	●	-0.6	5.6	1.1	2.4	0.0	45	2150	...	2710	...
23	●	-1.1	3.3	-2.8	0.4	0.0	20	2170	...	2730	...
24	R	-3.9	0.6	-2.8	-2.2	0.0	0	2170	...	...	...
25	C	-6.1	5.6	-2.8	0.6	3.4	30	2200	1.6	2760	2.6
26	C	-2.8	4.4	-1.1	0.0	0.2	35	2235	0.1	2795	0.2
27	C	-6.1	8.9	-1.1	2.4	20.2	25	2260	10.3	2820	16.0
28	●	-2.2	11.7	1.1	4.3	44.9	25	2285	23.2	2845	35.9
Mar. 1	S	-3.9	1.1	-2.2	-1.2	0.0	5	2290	...	2850	...
2	●	-3.3	1.1	-0.6	-0.8	0.0	5	2295	...	2855	...
3	●	-2.2	4.4	-0.6	1.0	0.0	35	2330	...	2890	...
4	●	-2.8	8.3	-4.4	2.1	12.0	30	2360	6.7	2920	10.1
5	●	-5.6	3.3	-1.7	-1.3	0.0	20	2390	...	2940	...
6	●	-6.1	2.8	-2.8	-0.8	0.0	15	2395	...	2955	...
7	R	-2.8	2.2	1.7	0.4	0.0	20	2415	...	2975	...
8	●	0.0	3.3	-0.6	1.5	0.0	30	2445	...	3005	...
9	S	-0.6	1.1	-5.0	-1.3	0.0	5	2455	...	3010	...
10	S	-6.7	1.1	-6.1	-3.2	0.0	5	2455	...	3015	...
11	S	-8.3	0.6	-5.0	-3.0	0.0	0	2455	...	3015	...
12	●	-5.0	3.3	-3.3	-0.7	0.0	25	2480	...	3040	...
13	●	-4.4	7.2	0.6	2.5	4.8	35	2515	3.1	3075	4.4
14	●	0.0	6.7	-0.6	2.9	4.1	40	2555	2.7	3115	3.7
15	●	-1.7	9.4	1.7	3.8	1.0	35	2590	0.7	3150	0.9
16	S	-1.7	3.9	-0.6	1.3	0.0	30	2620	...	3180	...

TABLE XII (CONTINUED)

Date	Wear- ther	Temperature in C			Daily 5 Hours	Leafing		Accum. 5 Hours	Cor- rected DU	Flowering	
		Min. or 6:00 A.M.	Max. 1:30 P.M.	10:00 P.M.		Ave.	Accum. 5 Hours				Cor- rected DU
1931											
Mar. 17	☉	-1.1	7.2	0.0	3.2	6.2	35	2655	+4.4	3215	5.9
18	S ☉	-0.6	4.4	0.6	2.0	0.0	30	2685	...	3245	...
19	R ☉	0.0	0.6	-0.6	-0.8	0.0	0	2685	...	3245	...
20	☉	-4.4	6.7	-1.7	1.6	10.6	26	2710	+7.7	3270	10.1
21	☉	-2.8	10.6	0.6	4.2	32.6	30	2740	+24.5	3300	31.6
22	☉	-1.7	11.7	3.9	5.2	25.9	40	2780	19.9	3340	25.4
23	☉	-1.1	14.4	3.9	7.7	68.2	55	2835	54.6	3395	67.5
24	R ☉	3.3	7.8	3.3	5.3	1.0	95	2930	0.8	3490	1.0
25	R ☉	2.2	4.4	1.7	2.9	0.0	50	2980	...	3540	...
26	☉	0.6	2.8	0.6	1.7	0.0	25	3005	...	...	...
27	☉	0.6	11.1	7.2	7.2	26.9	35	3040	24.2	...	26.9
28	R ☉	6.1	12.8	0.6	7.6	45.4	30	3070	40.9	...	45.4
29	☉	-1.1	0.6	-1.1	-0.2	0.0	0	3070	...	...	...
30	☉	-1.1	4.4	1.1	1.8	0.0	30	3100	...	...	...
31	☉	-0.6	10.0	2.8	5.1	16.6	45	3145	15.4	...	16.6
Apr. 1	R ☉	1.1	2.8	0.0	1.5	0.0	20	3165	...	...	...
2	☉	-0.6	9.4	...	5.0	24.2	40	3205	23.0	...	24.2
3	R ☉	1.7	5.6	...	3.5	0.0	60	3265	...	...	...
4	☉	1.1	15.0	...	7.1	83.5	40	3305	81.0	...	83.5
5	☉	-2.8	9.4	...	4.0	36.2	40	3345	35.5	...	36.2
6	☉	0.0	6.1	...	2.4	1.0	40	3385	1.0	...	1.0
7	☉	-2.8	12.8	2.8	6.1	53.5	50	3435	53.0	...	53.0
8	☉	1.7	20.6	12.8	13.3	143.3	15	3450	142.6	...	142.6
9	☉	10.0	25.6	14.4	17.9	178.5	0	3450	177.6	...	140.0
Fl. 10	R ☉	10.0	15.0	7.8	11.0	57.2	15	3465	57.0	...	...

TABLE XII (CONTINUED)

Date	Weather	Temperature in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Ave.			Accum. 5 Hours	Corrected DU	Accum. 5 Hours	Corrected DU
1931											
Apr. 11	R	3.9	12.8	2.8	7.2	60.7	40	3505	60.7		...
12	O	-0.6	20.6	11.7	12.1	131.5	...	...	131.5		...
13	O	7.8	25.0	10.6	16.1	166.6	...	...	166.6		...
14	C	6.7	18.3	5.6	11.5	102.8	...	...	102.8		...
15	O	2.8	16.7	4.4	9.2	91.5	...	...	91.5		...
16	O	0.6	23.9	11.1	14.2	153.0	...	...	153.0		...
17	R	8.3	23.3	8.9	14.4	142.4	...	...	142.4		...
18	O	2.8	20.6	7.2	12.1	125.2	...	...	125.2		...
19	O	4.4	26.7	14.4	17.5	184.0	...	...	184.0		...
20	O	12.2	26.7	16.1	19.4	150.0	...	...	150.0		...
Totals		...	...	...	...	2368.8	...	...	2136.8	...	821.8

TABLE XIII

WEATHER AND DEVELOPMENTAL UNITS OF WHITE ELM
OBERLIN, OHIO

Date	Weather	Min. or 6:00 A.M. C	Max. or 1:30 P.M. C	10:00 P.M. C	Ave. C	DU	Daily 5 Hours	Leafing		Flowering	
								Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1932											
Dec. 23	R ●	-1.1	11.7	10.2	7.8	16.0	...	610	1.0	1405	3.2
24	R ●	8.9	16.1	11.7	12.8	75.0	...	612	4.5	1410	15.0
25	0	10.0	17.2	6.1	11.4	83.0	...	630	5.0	1425	17.0
26	0	1.1	11.1	1.1	4.7	34.0	...	655	2.2	1450	7.1
		-4.4									
28	0	-6.1	12.2	2.2	3.9	35.0	...	695	2.4	1490	7.7
29	0	-2.8	13.3	7.2	6.8	42.0	...	715	2.9	1510	9.2
1933											
Jan. 2	0	-4.4	4.4	-0.6	0.0	0.0	20	815	...	1610	...
3	●	-2.2	4.4	4.4	1.1	0.0	80	895	...	1690	...
4	●	4.4	11.7	1.1	6.1	11.8	30	925	1.3	1720	3.4
5	●	-3.9	5.6	1.7	1.1	0.0	30	955	...	1750	...
6	●	-2.2	7.8	7.8	5.3	7.9	50	1005	0.9	1800	2.4
7	●	7.8	8.9	-1.1	4.4	3.1	35	1040	0.4	1835	1.0
8	●	-3.9	5.6	1.1	1.1	0.0	30	1070	...	1865	...
		1.1									
10	●	-3.3	5.6	7.2	2.8	0.0	70	1140	...	1935	...
11	R ●	7.2	10.0	-5.6	3.9	4.8	30	1170	0.7	1965	1.8
		-9.4									
14	●	-5.0	5.6	-2.8	0.0	0.0	20	1190	...	1985	...
15	●	-6.1	7.8	2.8	1.1	1.9	40	1230	0.3	2025	0.8

TABLE XIII (CONTINUED)

Date	Wear- ther	Min. or 6:00 A.M. C	Max. or 1:30 P.M.	10:00 P.M. C	Ave. C	DU	Daily 5 Hours	Leafing Accum. 5 Hours	Cor- rected DU	Flowering Accum. 5 Hours	Cor- rected DU
1933 Jan. 16	☉	-0.6	7.2	6.1	5.0	2.4	60	1290	0.4	2085	1.0
17	☉	6.1	7.8	-0.6	3.9	0.0	40	1330	...	2125	...
18	R ☉	-1.7	6.1	6.7	2.8	0.0	75	1405	...	2200	...
19	☉	6.7	12.8	0.6	8.3	23.3	35	1440	4.9	2235	11.7
20	☉	-2.2	6.7	0.6	2.2	3.7	25	1465	0.8	2260	1.9
21	☉	0.6	11.7	8.3	6.7	21.1	35	1500	4.6	2395	11.2
22	R ☉	8.3	18.9	8.9	12.5	121.0	20	1520	27.8	2315	65.3
23	☉	1.7	7.8	-1.1	3.3	1.9	25	1545	0.4	2340	1.0
24	☉	-4.4	9.4	1.7	2.8	16.2	30	1575	3.9	2370	9.2
25	R ☉	0.6	6.7	3.3	3.9	0.0	60	1655	...	2430	...
26	R ☉	1.1	3.3	1.7	2.2	0.0	35	1670	...	2465	...
27	R ☉	1.1	2.8	-1.7	0.6	0.0	15	1685	...	2480	...
31	☉	-1.1	7.8	2.2	3.3	4.6	40	1725	1.3	2520	2.9
Feb. 1	R ☉	1.7	11.7	3.3	5.0	7.3	35	1760	2.2	2555	4.8
2	☉	-1.1	3.3	-3.9	0.1	0.0	10	1770	...	2565	...
3	☉	-5.0	5.9	-3.9	-0.7	0.0	20	1790	...	2585	...
4	☉	-5.6	2.8	-9.4	-4.0	0.0	10	1800	...	2595	...
6	☉	-13.9	1.1	0.6	-3.1	0.0	15	1815	...	2610	...
7	RS ☉	-1.1	6.7	0.6	0.1	0.0	30	1845	...	2640	...
13	R ☉	-11.7	7.8	2.2	2.6	6.6	40	1885	2.2	2680	4.8
14	☉	1.1	5.0	-1.7	0.7	0.0	30	1915	...	2710	...

TABLE XIII (CONTINUED)

Date	Weather	Min. or 6:00 A.M. C	Max. or 1:30 P.M. C	10:00 P.M. C	Ave. C	DU	Daily 5 Hours	Leafing		Flowering	
								Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1933											
Feb. 16	0	-6.7	4.4	3.9	0.2	0.0	60	1975	...	2770	...
17	0	-1.1	5.6	-2.2	0.9	0.0	35	2010	...	2805	...
18	0	-6.7	5.0	-2.8	-0.7	0.0	30	2040	...	2835	...
19	R	-6.1	12.8	6.1	6.7	34.4	40	2080	14.4	2875	28.2
20	0	-0.6	7.8	0.6	2.2	6.4	30	2110	2.8	2905	5.3
21	0	-6.1	0.0	-3.3	-2.6	0.0	10	2120	...	2915	...
22	0	-4.4	15.0	8.3	6.8	62.5	35	2155	28.7	2950	53.4
23	0	1.7	10.0	2.8	5.6	25.5	35	2190	12.0	2985	22.2
24	R	0.6	11.1	5.0	6.1	30.9	65	2255	15.8	3050	27.8
25	R	1.7	10.0	-1.1	4.9	7.8	30	2285	4.1	3080	7.1
26	0	-2.2	2.2	-3.9	-0.8	0.0	10	2295	...	3090	...
27	0	-5.6	2.2	-3.3	-1.6	0.0	15	2310	...	3105	...
28	0	-5.0	6.7	2.8	1.6	1.0	35	2345	0.5	3140	0.9
Mar. 3	S	-1.1	2.2	-1.1	0.3	0.0	10	2355	...	3150	...
4	S	-2.2	-0.6	-2.2	-1.9	0.0	0	2355	...	3150	...
		-4.4									
6	0	-8.3	10.6	3.3	1.0	15.2	30	2385	8.7	3180	14.3
7	0	-2.2	6.7	-0.6	2.5	0.0	20	2405	...	3200	...
8	RS	-1.1	7.2	0.0	2.3	0.0	20	2425	...	3220	...
9	0	-4.4	1.1	-8.9	-3.9	0.0	5	2430	...	3225	...
10	0	-13.3	-5.0	-11.1	-9.0	0.0	0	2450	...	3225	...
		-12.8									
12	0	-6.7	11.1	5.6	2.6	24.7	50	2480	15.1	3275	23.8
13	R	4.4	10.6	10.0	8.5	21.7	25	2505	13.7	3300	21.0
14	R	6.1	14.4	3.3	8.1	48.6	30	2535	31.6	3330	47.6

TABLE XIII (CONTINUED)

Date	Wea- ther	Min. or 6:00 A.M. C	Max. or 1:30 P.M.	10:00 P.M. C	Ave. C	DU	Daily 5 Hours	Leafing		Flowering	
								Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1933											
Mar. 15	☉	0.0	-1.1	-3.3	-2.8	0.0	0	2535	...	3330	...
16	☉	-8.9	7.2	1.7	-0.1	15.1	35	2570	10.0	3365	14.8
17	☉	-2.2	15.0	6.7	9.3	76.1	50	2620	52.5	3415	75.3
18	R ☉	4.4	6.7	-0.6	3.3	0.0	40	2660	...	3455	...
19	R ☉	-1.1	3.5	2.8	1.8	0.0	40	2700	...	3495	...
20	R ☉	1.7	10.0	5.6	7.1	15.7	50	2750	11.8	3545	15.6
21	S ☉	0.6	-1.1	-2.2	-1.2	0.0	0	2750	...	...	...
24	S ☉	-3.3	1.7	-1.1	-0.8	0.0	10	2760	...	...	...
25	S ☉	-3.3	2.8	0.0	0.0	0.0	10	2770	...	...	...
26	S ☉	-2.2	3.9	-1.1	0.7	0.0	20	2790	...	...	...
27	SR ☉	-2.8	10.6	4.4	3.6	11.5	30	2820	9.1	...	11.5
28	☉	-1.7	3.9	-2.2	0.0	0.0	25	2845	...	...	...
29	☉	-6.1	8.9	-0.6	1.5	23.1	25	2870	18.9	...	23.1
30	☉	-1.1	14.4	-7.2	6.9	59.3	20	2890	48.6	...	59.3
31	R ☉	7.8	19.4	12.8	13.7	117.0	5	2895	97.1	...	117.0
Apr. 1	☉	11.7	13.9	6.1	10.1	54.0	40	2935	45.9	...	54.0
Fl. 2	R ☉	5.6	11.7	5.0	7.7	59.3	60	2995	52.2	...	59.3
3	R ☉	2.8	10.6	2.2	5.6	22.5	50	3045	20.2	...	...
4	☉	1.1	8.3	2.8	4.5	5.1	60	3105	4.7	...	...
5	☉	1.7	17.8	12.8	7.9	98.1	20	3125	91.2	...	...
6	R ☉	10.0	16.7	5.0	10.0	64.0	40	3165	60.2	...	...
7	S ☉	3.3	4.4	0.6	2.8	0.0	50	3215	...	...	...
8	☉	-1.1	8.3	2.2	4.1	0.0	40	3255	...	...	...
9	☉	1.1	16.1	5.0	7.6	78.5	50	3305	76.2	...	...
10	R ☉	3.3	28.9	14.4	15.3	135.1	10	3315	131.0	...	...

TABLE XIII (CONTINUED)

Date	Weather	Min. or 6:00 A.M. C	Max. or 1:30 P.M.	10:00 P.M. C	• Ave. C	DU	Daily 5 Hours	Leafing		Flowering	
								Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1933											
Apr. 11	R	13.3	15.6	2.8	8.6	53.5	30	3345	52.4	...	...
12	O	0.0	14.4	5.6	7.3	74.9	40	3385	74.2	...	...
13	O	2.8	18.3	7.8	10.4	110.0	20	3405	108.9	...	...
14	R	6.7	20.0	10.0	13.0	113.0	10	3415	111.9	...	...
15	R	4.4	7.8	7.2	6.7	4.1	80	3495	4.1	...	...
16	R	5.0	15.6	8.9	11.4	81.1	...	...	81.1	...	...
17	O	6.7	18.9	7.8	11.8	103.5	...	...	103.5	...	...
18	R	7.8	10.6	8.3	9.2	20.7	...	...	20.7	...	...
19	R	5.6	9.4	6.7	7.1	4.6	...	...	4.6	...	...
20	O	6.7	15.0	10.0	10.3	78.7	...	...	78.7	...	...
21	O	5.6	17.8	3.3	8.5	82.5	...	...	82.5	...	...
22	O	0.6	8.3	-0.6	3.2	15.4	...	...	15.4	...	...
23	O	-2.2	15.0	4.4	6.8	79.1	...	...	79.1	...	...
24	O	3.3	21.7	11.1	12.9	143.8	...	...	143.8	...	...
25	R	8.9	13.3	2.2	8.3	45.1	...	...	45.1	...	...
26	O	0.6	6.7	1.1	3.4	2.2	...	...	2.2	...	...
27	O	-1.1	11.7	3.9	5.7	36.4	...	...	36.4	...	...
28	O	2.2	22.2	15.0	14.3	172.7	...	...	172.7	...	...
29	O	8.9	30.6	15.6	19.9	177.9	...	...	177.9	...	...
30	O	14.4	27.2	17.2	19.7	229.1	...	...	229.1	...	...
First trees leaf- ing											
Last trees											
Totals							3034.9		2342.3		863.9

TABLE XIV
WEATHER AND DEVELOPMENTAL UNITS FOR WHITE ELM
OBERLIN, OHIO

Date	Weather	Temperatures in C			DU	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 10:00 P.M.	Ave.		Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1933									
Dec. 5	☉	5.6	11.7	7.6	35.0	340	1.0	940	3.8
15	R ☉	1.1 -7.8	18.3	4.4	93.0	430	3.7	1030	12.1
17	R ☉	4.4 -1.1	12.8	5.1	18.0	495	0.9	1095	1.5
18	☉	0.0	11.1	5.0	32.0	520	1.6	1120	4.5
23	☉	-2.2 -1.7	17.2	10.0	120.0	600	7.2	1200	19.2
24	R ☉	7.2 -3.9	12.8	7.2	28.0	620	1.7	1210	3.5
1934									
Jan. 11	☉	-5.0	6.7	-0.6	2.6	925	0.3	1525	0.6
15	☉	-2.8	6.7	0.6	1.4	990	0.2	1590	0.3
19	☉	-3.9	8.3	1.7	10.3	1015	1.2	1615	2.7
20	☉	-6.1	9.4	2.8	17.3	1065	2.2	1665	4.7
21	☉	-2.2	16.7	8.0	83.5	1095	11.7	1695	23.4
22	R ☉	1.1	11.7	6.1	10.3	1135	1.6	1735	3.0
24	☉	-6.7	8.3	4.4	19.9	1220	3.4	1820	6.4
25	☉	5.6	8.9	3.3	1.0	1290	0.2	1890	0.3
26	☉	-3.3	4.4	0.0	0.5	1310	0.1	1910	0.2
27	☉	0.0	8.9	5.6	13.0	1370	2.4	1970	4.9
Mar. 1	☉	-12.2	5.6	-1.1	0.7	1540	0.2	2140	0.3

TABLE XIV (CONTINUED)

Date	Wea- ther	Temperatures in C			DU	Leafing		Flowering	
		Min. or 6:00 A.M.	Max. or 1:30 P.M.	Ave. 10:00 P.M.		Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1934									
Mar. 3	R ☉	1.7	7.2	3.9	0.0	1660	0.0	2260	0
4	R ☉	3.9	12.8	5.9	21.8	1710	6.1	2310	15.5
5	R ☉	3.9	11.1	-2.8	5.8	1750	1.8	2350	3.5
13	☉	0.0	12.8	-7.8	4.4	1800	9.6	2400	18.0
15	☉	-10.0	6.1	1.1	0.8	1840	2.8	2440	5.0
16	☉	1.1	15.6	1.7	8.3	1870	32.3	2470	57.7
17	R ☉	1.7	19.4	-6.1	8.6	1900	30.8	2500	54.7
19	☉	-13.9	5.0	-7.2	2.4	1920	0.9	2520	1.5
20	☉	-7.2	4.4	1.1	0.8	1945	0.0	2545	0
21	R ☉	1.1	9.4	-8.9	1.4	1975	0.4	2575	0.7
25	☉	-8.9	4.4	-5.6	-1.4	2015	0.0	2615	0
29	☉	-5.6	13.3	-0.6	5.0	2065	23.5	2665	39.7
30	☉	-0.6	11.1	4.4	5.6	2095	16.4	2695	27.2
31	☉	4.4	19.4	1.7	11.1	2125	48.0	2725	79.0
Apr. 1	☉	1.7	16.7	5.6	10.0	2155	44.3	2755	73.1
2	☉	5.6	19.4	4.4	12.2	2185	59.2	2785	97.0
3	R ☉	4.4	22.2	2.2	130.1	2215	63.8	2815	102.8
4	R ☉	2.2	9.4	6.7	26.2	2285	13.6	2885	21.5
5	R ☉	6.7	19.4	2.8	115.2	2315	62.2	2915	96.8
6	R ☉	2.8	14.4	1.7	8.3	2345	23.1	2945	35.7
7	☉	1.7	15.0	2.2	8.3	2375	24.9	2975	38.0
Flower- ing 8	☉	2.2	16.7	3.3	10.0	2400	37.7	3000	28.6
9	☉	3.3	21.1	8.9	149.1	2415	87.9	...	...
10	R ☉	8.9	20.6	7.2	135.0	2430	80.1	...	...
15	R ☉	-0.6	11.1	2.8	18.5	2545	12.0	...	...

TABLE XIV (CONTINUED)

Date	Weather	Temperatures in C			DU	Leafing		Flowering	
		Min. 6:00 A.M.	Max. or 1:30 P.M.	Ave. 10:00 P.M.		Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1934									
Apr. 16	R ☉	2.8	13.9	2.8	47.9	2585	32.1	...	...
17	O	2.8	19.4	7.2	122.4	2605	83.3	...	...
18	O	7.2	20.0	7.8	133.8	2625	92.3	...	...
19	O	7.8	16.7	1.7	73.7	2650	41.9	...	...
20	O	1.7	8.3	-1.7	1.4	2685	1.0	...	...
21	S ☉	-1.7	9.4	-1.1	1.2	2715	0.9	...	...
22	R ☉	-1.1	8.9	3.3	0.7	2785	0.5	...	...
23	R ☉	3.3	18.9	2.8	125.3	2810	98.4	...	...
24	SR ☉	2.8	12.2	-1.1	24.6	2840	19.7	...	...
25	O	-1.1	10.0	0.6	27.0	2865	21.9	...	...
26	O	0.6	12.2	-1.1	15.8	2895	13.1	...	...
27	O	-1.1	7.8	-3.9	1.0	2925	0.8	...	...
28	O	-3.9	12.8	3.3	61.4	2990	52.8	...	...
29	O	3.3	21.7	7.8	145.6	3005	127.4	...	...
30	O	7.8	22.8	7.8	167.5	3010	147.4	...	...
May 1	O	7.8	24.4	10.0	172.8	3015	152.1	...	...
2	O	10.0	27.8	6.7	175.0	3020	155.7	...	...
3	O	6.7	27.2	11.1	169.4	3020	150.8	...	...
4	O	11.1	31.1	15.6	22.2	3020	162.6	...	...
5	O	15.6	28.9	13.3	235.2	3020	209.3	...	...
6	O	13.3	30.6	...	102.8	3020	91.5	...	...
Totals		...	...	...	3872.9	...	2376.5	...	887.4

TABLE XV
WEATHER AND DEVELOPMENTAL UNITS FOR WHITE ELM
OBERLIN, OHIO

Date	Weather	Temperatures in C			DU	Daily 5 Hours	Leafing		Flowering	
		Min. 6:00 A.M.	Max. 1:30 P.M.	Mean			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1935										
Jan.										
2	☉	-12.2	2.2	-2.2	0.0	25	425	...	1430	...
3	S ☉	-0.6	2.2	-2.2	0.0	20	445	...	1450	...
4	☉	-12.8	-2.2	-6.4	0.0	00	445	...	1450	...
5	☉	-8.5	10.0	3.9	12.0	70	505	0.6	1520	2.8
6	R ☉	5.0	8.3	6.7	4.8	90	605	0.3	1610	1.2
7	R ☉	5.0	10.6	8.6	28.8	50	655	2.0	1660	6.8
8	R ☉	6.1	10.6	8.3	3.6	30	685	0.3	1690	1.0
9	R ☉	3.9	9.4	6.7	1.2	60	745	0.1	1750	0.4
10	☉	3.9	10.0	5.0	16.1	40	785	1.4	1790	5.0
11	☉	-3.3	0.0	-2.5	0.0	0	785	...	1790	...
13	R ☉	-2.2	3.9	0.0	0.0	20	805	...	1810	...
17	☉	-0.6	2.2	1.1	0.0	40	845	...	1850	...
18	☉	-7.8	-1.1	-3.9	0.0	0	845	...	1850	...
19	☉	-5.0	0.6	-1.1	0.0	0	845	...	1850	...
20	R ☉	0.0	5.6	3.9	0.0	70	915	...	1920	...
21	R ☉	4.4	6.7	2.2	0.0	40	955	...	1960	...
Feb.										
1	☉	-8.9	4.4	-1.1	0.0	20	975	...	1980	...
2	☉	-3.3	3.3	0.0	0.0	20	995	...	2000	...
3	☉	-3.3	1.7	-5.0	0.0	10	1005	...	2010	...
5	☉	-5.0	1.1	-11.7	0.0	5	1010	...	2015	...

TABLE XV (CONTINUED)

Date	Wea- ther	Temperatures in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Mean			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1935											
Feb. 8	•	-3.3	2.8	0.0	0.3	0.0	30	1040	...	2045	...
9	•	-1.1	0.6	-3.3	-1.7	0.0	0	1040	...	2045	...
12	•	-3.9	5.6	-4.4	0.3	0.5	20	1060	0.1	2065	0.2
13	•	-6.1	5.6	2.8	1.4	0.0	40	1100	...	2105	...
14	R •	2.8	10.0	5.6	6.4	2.6	60	1160	0.4	2165	1.2
15	•	2.8	11.7	1.7	6.1	22.8	40	1200	3.6	2205	10.9
16	•	-1.1	0.6	-3.9	-1.7	0.0	0	1200	...	2205	...
18	•	-5.0	2.8	1.7	0.0	0.0	20	1220	...	2225	...
19	•	-1.1	2.2	3.9	-0.6	0.0	20	1240	...	2245	...
20	•	-5.6	2.2	-8.9	-2.8	0.0	10	1250	...	2255	...
23	•	-7.8	-1.1	-6.7	-4.2	0.0	0	1250	...	2255	...
24	•	-6.7	6.7	2.2	1.9	3.6	40	1290	0.6	2295	1.9
25	R •	1.1	8.3	-2.2	1.7	0.0	40	1330	...	2335	...
Mar. 1	•	-4.4	5.6	2.2	2.2	0.0	40	1370	...	2375	...
2	•	1.7	11.1	4.4	5.6	32.2	50	1420	6.4	2425	19.0
3	•	-1.1	5.6	2.8	1.7	0.7	30	1450	0.1	2455	0.4
4	•	2.8	17.8	8.9	10.6	99.4	20	1470	20.9	2475	61.6
5	•	8.9	20.0	11.1	12.8	105.6	0	1470	22.2	2475	65.5
6	•	1.7	5.6	-0.6	2.8	0.0	40	1510	...	2515	...
8	•	-5.6	-0.6	-7.8	-3.9	0.0	10	1520	...	2525	...
9	•	-9.4	6.1	2.8	1.1	2.9	40	1560	0.7	2565	1.8
10	R •	2.2	7.2	7.2	5.6	0.0	60	1620	...	2625	...
11	R •	3.9	3.9	-1.1	-0.6	0.0	30	1650	...	2655	...
12	•	-4.4	1.1	-3.3	-2.2	0.0	10	1660	...	2665	...
13	•	-6.7	4.4	0.0	-0.6	0.0	30	1690	...	2695	...

TABLE XV (CONTINUED)

Date	Weather	Temperature in C			DU	Daily 5 Hours	Leafing		Flowering	
		Min. 6:00 A.M.	Max. or 1:30 P.M.	Mean 10:00 P.M.			Accum. 5 Hours	Corrected DU	Accum. 5 Hours	Corrected DU
1935										
Mar. 14	☉	-3.9	3.9	0.0	0.0	30	1720	...	2725	...
15	☉	0.0	19.4	15.6	12.8	10	1730	43.8	2735	111.7
16	☉	11.7	20.0	15.6	12.8	0	1730	45.2	2735	116.1
18	☉	-6.1	5.6	3.3	1.7	50	1780	1.2	2785	3.2
19	R ☉	1.7	10.6	6.7	6.1	70	1850	4.2	2855	10.3
20	☉	3.3	15.6	10.6	10.0	30	1880	24.5	2885	59.1
21	☉	5.0	20.0	4.4	11.7	50	1930	34.6	2935	81.6
22	☉	1.7	20.6	11.1	12.2	20	1950	42.4	2955	98.5
23	☉	6.1	18.9	5.0	10.6	30	1980	30.9	2985	79.2
24	☉	-1.1	8.9	2.8	4.4	50	2030	0.8	3035	1.7
25	☉	0.6	8.3	-0.6	3.9	40	2070	0.2	3075	0.5
26	C ☉	-2.2	7.2	0.0	2.8	30	2100	0.8	3105	1.7
27	☉	-1.1	18.3	10.0	9.4	30	2130	39.9	3135	84.4
28	☉	1.7	17.2	2.8	8.9	30	2160	36.2	...	...
29	☉	0.0	13.9	5.6	6.9	40	2200	18.8	...	...
30	☉	0.0	10.6	2.2	5.6	40	2240	8.4	...	...
31	☉	1.1	3.3	1.7	2.2	30	2270	0.0	...	...
Apr. 1	☉	1.1	7.2	2.2	4.4	40	2310	0.0	...	...
2	☉	1.7	8.9	2.2	4.4	30	2340	1.0	...	...
3	C ☉	-1.7	7.2	1.7	2.8	40	2380	0.7	...	...
4	☉	-1.7	8.9	1.7	4.4	30	2410	9.9	...	...
5	☉	1.1	6.1	1.1	3.1	30	2440	0.0	...	...
6	S ☉	-1.1	10.0	1.7	4.4	20	2460	5.6	...	...
7	SC ☉	-0.6	8.9	1.1	4.4	30	2490	0.3	...	...

TABLE XV (CONTINUED)

Date	Wea- ther	Temperatures in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. 6:00 A.M.	Max. or 1:30 P.M.	10:00 P.M.	Mean			Accum. 5 Hours	Cor- rected DU	Accum. 5 Hours	Cor- rected DU
1935											
Apr. 8	●	0.0	3.3	1.7	1.7	0.0	20	2510	0.0	...	...
9	●	0.6	7.2	2.8	3.3	5.5	30	2540	3.6	...	...
10	●	-1.7	15.0	5.6	7.8	76.8	40	2580	51.5	...	...
11	R ●	2.8	12.8	7.2	8.3	21.4	50	2630	15.0	...	...
12	R ●	4.4	15.0	1.7	8.9	40.1	30	2660	28.5	...	...
13	C ●	1.7	7.2	0.0	3.3	0.0	30	2690	0.0	...	...
14	●	-2.8	15.0	7.2	6.7	76.8	30	2720	56.8	...	...
15	●	0.0	1.7	-6.7	-1.1	0.0	10	2730	0.0	...	...
16	●	-7.2	1.7	0.0	-1.4	0.0	10	2740	0.0	...	...
17	●	-1.7	6.1	0.0	2.8	0.0	20	2760	0.0	...	...
18	●	-2.2	15.6	3.3	8.1	76.8	30	2790	59.1	...	...
19	●	3.3	20.0	5.0	11.1	108.0	40	2830	85.3	...	...
20	●	1.7	19.4	6.1	7.8	93.6	40	2870	76.8	...	...
21	●	2.2	16.1	3.9	8.3	79.2	30	2900	65.7	...	...
22	C ●	-0.6	14.4	6.7	7.8	48.0	40	2940	40.8	...	...
23	C ●	2.8	17.2	6.7	10.3	110.4	40	2980	96.0	...	...
24	C ●	3.9	16.7	4.4	9.4	91.2	30	3010	80.3	...	...
25	●	0.6	20.0	6.7	10.6	86.1	40	3050	77.5	...	...
26	●	2.2	25.6	13.3	16.1	153.8	10	3060	138.4	...	...
27	R ●	10.6	22.8	12.8	16.1	146.9	0	3060	132.2	...	...
28	●	8.9	20.6	10.0	14.4	115.8	0	3060	105.4	...	...
29	R ●	8.3	13.9	7.8	15.0	43.2	40	3100	39.7	...	...
30	C ●	2.2	8.3	3.3	4.7	0.0	50	3150	0.0	...	...
May 1	C ●	0.0	11.7	3.2	6.1	9.6	40	3190	9.1	...	...
2	R ●	1.7	7.2	4.4	5.0	0.0	80	3270	0.0	...	...

TABLE XV (CONTINUED)

Date	Weather	Temperatures in C				DU	Daily 5 Hours	Leafing		Flowering	
		Min. or A.M.	Max. or 1:30 P.M.	10:00 P.M.	Mean			Accum. 5 Hours	Cor-rected DU	Accum. 5 Hours	Cor-rected DU
1935											
May											
3	R	3.3	18.9	3.3	10.6	76.8	30	3300	74.5	...	...
4	C	1.1	7.8	4.4	5.6	0.0	80	3380	0.0	...	...
5	C	3.3	10.0	5.6	6.9	2.3	60	3440	2.3	...	...
6	R	4.4	9.4	5.6	6.9	0.0	70	3520	0.0	...	...
7	C	4.4	12.8	5.6	7.8	36.0	40	...	36.0	...	...
8	C	0.6	18.9	9.4	11.7	110.4	20	...	110.4	...	...
9	R	7.8	23.9	12.2	16.1	134.4	10	...	134.4	...	...
10	C	8.9	18.9	7.8	12.8	110.4	30	...	110.4	...	...
11	C	3.9	20.6	10.0	13.0	103.7	20	...	103.7	...	...
12	R	7.2	16.1	10.6	12.2	84.0	10	...	84.0	...	...
Leaf 13	C	8.9	20.0	12.8	13.9	67.2	...	...	67.2	...	...
Totals						3400.4			2293.7		827.7

For a long time it was found impossible to bring the thermoconstants for flowering into any sort of agreement with each other. In all the computation it was assumed, merely for working purposes, that the responses of the flower buds to temperature were of just the same nature as those of the much better understood leaf buds. The experimental evidence was too scanty to make any other assumption worth the time needed in computation. Finally it occurred to the author that perhaps one reason why flower buds opened so much earlier than leaf buds was that they went into dormancy sooner. On this new assumption the November weather conducive to after-ripening was computed and added to the accumulated totals for flowering. The thermoconstants resulting from this new correction agreed rather closely, as the Table XVI shows. It is not felt that this fairly close agreement more than suggests that flower buds go into dormancy sooner than do leaf buds, but it is felt that that suggestion is worth consideration.

These thermoconstants disagree more than might be desired. However, the known errors in the method are sufficient to explain all the disagreement there is, and further, it should be noted that in 1933 the first Oberlin white elms to leaf began at a thermoconstant of 2078 DU, the stock tree at 2342.3 DU, and the slowest healthy elms at 2552 DU. This is a decidedly greater variation than was found for the stock tree during the five very different years.

TABLE XVI

THERMOCONSTANTS FOR WHITE ELM

COMPUTATION FROM PHENOLOGICAL DATA
FOR OBERLIN, OHIO

To Flowering				
Year	Date of Flowering	Total of Mean Positive Temperature from Jan. 1 °C	Total DU Not Corrected for Degree of After-ripening	Total DU Corrected for Degree of After-ripening
1930	Mar. 18	163.8	1809	862.4
1931	Apr. 9	140.7	1074	821.8
1933	Apr. 2	180.0	818	863.9
1934	Apr. 8	174.7	1550	887.4
1935	Mar. 27	169.2	936	827.7

TABLE XVI (CONTINUED)

To Leafing				
Year	Date of Leafing	Total of Mean Positive Temperature from Jan. 1 °C	Total DU Not Corrected for Degree of After-ripening	Total DU Corrected for Degree of After-ripening
1930	Apr. 20	428.1	3907.4	2379.0
1931	Apr. 20	338.8	2388.8	2136.8
1933	Apr. 29	455.5	3034.8	2342.3
1934	May 6	455.7	3872.9	2376.5
1935	May 13	569.0	3400.4	2293.7

Attention was given to the work of MacLagan (45), 1933, who approached this whole question from quite a different angle. He found that time of flowering was determined by the temperature obtained during critical periods of narrow belts of time. This may be true for the plants MacLagan investigated, but it appears not to be true for white elm. The effect of after-ripening might be considered as occurring during a critical period, but with that possible exception, all the author's results indicate that flowering, as also leafing, is determined by the accumulation of the experience of effective warmth and that no period during the season is more critical than any other.

CONCLUSIONS AND SUMMARY

After working for eight years on the problems of dormancy and leafing in white elm, using potted seedlings as most of the material, the author has come to the following conclusions:

1. Dormancy in white elm is due to the response of mature tissue to the external stimulus of shortening day, and the response is hastened by progressive cooling and by warm days alternating with cold nights.
2. Cold-hardiness is due to progressive chilling or warm days alternating with cold nights or both acting on mature tissues.
3. The period of midrest, or the period of no response, is over and after-ripening begins in early December in leaf buds and probably about the first of November in flower buds.
4. After-ripening is due to the accumulation of the experience of temperatures around 5° C. to a total of about 3000 degree-hours for seedlings and about 3500 degree-hours for adult trees. There is wide variation in the date when the accumulation of this total is complete, but 100 per cent effectiveness of warmth is not attained until that time. Freezing as a shock is not essential.
5. Under natural conditions warmth is the only important external factor determining time of leafing in white elm.
6. The accumulation of the experience of warmth begins at a much reduced efficiency as soon as after-ripening has reached a certain minimum, and its efficiency increases progressively as after-ripening more and more closely approaches completion.
7. The curve of the velocity of development at different temperatures was determined by experiment at constant temperatures. The curve shows the actual threshold at near 7° C., the theoretical or "hyperbolic" threshold at 9° C. This is the curve of the velocity of development toward leafing; not a curve of the speed of growth.
8. The effect of sunshine in heating the white elm buds is very marked. On the average, the increase in bud temperature during a sunshiny day is about 6° C., but the amount of increase varies with variation in wind velocity, degree

of cloudiness, time of day and time of year. As leafing approaches and the buds swell with the exposure of more green in proportion to dark brown, the heating effect of sunshine shows a rather sudden decrease.

9. The thermoconstant for flowering in white elm is about 850 DU, for leafing in seedlings is about 1500 DU, and for leafing in adult trees is about 2300 DU.
10. Computation of thermoconstants from thermograph records yielded results very similar to those obtained by experiment. The totals, as determined for five years at Oberlin, were 850 DU $\pm$ 4.1 per cent for flowering, and 2300 DU $\pm$ 5.3 per cent for leafing. The variation for the five years, as so found for a single tree, was decidedly less than the variation among neighboring individuals of this species in the same year.

LITERATURE CITED

1. Abbe, C. A first report on the relation between climate and crops. U. S. Dept. Agric., Weath. Bur. Bull. 36. 1905.
2. Abbott, O. Chemical changes at beginning and ending of rest period in apple and peach. Bot. Gaz. 76: 167-84. 1923.
3. Adams, J. Some further experiments on the relation of light to growth. Amer. Jour. Bot. 12: 398-412. 1925.
4. Allard, H. A. Length of day in the natural and artificial distribution of plants. Ecology 13 (3): 221-34. 4 figs. 1932.
5. Becquerel, L. A. Des climats et de l'influence qu' exercent les sols boisés et non boisés. 566 pp. Paris, 1853.
6. Belehrádek, J. Temperature coefficients in biology. Biol. Rev. and Biol. Proc. Cambridge Phil. Soc. 5 (1): 30-58. 7 figs. 1930.
7. Brendel, F. Flora Peoriana: the vegetation in the climate of middle Illinois. 89 pp. Peoria, Ill., 1887.
8. Coville, F. V. The influence of cold in stimulating the growth of plants. Jour. Agric. Res. 20: 151-60. 1920.
9. Curtis, O. F. Stimulation of root growth in cuttings by treatment with chemical compounds. Cornell Univ. Agric. Exp. Sta. Mem. 14. 1918.
10. Davis, W. E. Primary dormancy, after-ripening, and the development of secondary dormancy in embryos of *Ambrosia trifida*. Amer. Jour. Bot. 17: 58-76. 1930.
11. Denney, F. E. Effect of thiourea upon bud inhibition and apical dominance in potato. Bot. Gaz. 81: 297-311. 1926.
12. _____. Chemical treatment for controlling the growth of buds of plants. Jour. Ind. and Engineer. Chem. 20: 578-81. 1928.
13. _____. Direct versus indirect effects upon potato amylase by chemicals which induce sprouting of dormant tubers. Contr. Boyce Thompson Inst. 4 (1): 53-63. 2 figs. 1932.
14. _____. Effect of potassium thiocyanate and ethylene chlorhydrin upon amylase activity. Contr. Boyce Thompson Inst. 5: 441-50. 3 figs. 1933.

15. Denney, F. E., and Lawrence Miller. Effect of Ethylene Chlorhydrin vapors upon dormant lilac tissues. Contr. Boyce Thompson Inst. 4: 513-28. 1 fig. 1932.
16. Denney, F. E., and Stanton, E. N. Localization of response of woody tissues to chemical treatments that break the rest period. Amer. Jour. Bot. 15: 337-44. 1928.
17. Dexter, S. T. Effect of several environmental factors on the hardening of plants. Plant Physiol. 8 (1): 123-39. 5 figs. 1933.
18. Doerfel, F. Über den Einfluss des Frostes und intermittierender Temperaturen auf die Keimung verschiedener Samen. Bot. Arch. 30 ($\frac{1}{2}$): 1-50. 1930.
19. Eckerson, S. A physiological and chemical study of after-ripening. Bot. Gaz. 55: 286-99. 1913.
20. Edwards, T. I. Temperature relations of seed germination. Quart. Rev. Biol. 7 (4): 428-43. 1 fig. 1932.
21. Ehlers, J. H. The temperature of leaves of Pinus in winter. Amer. Jour. Bot. 2: 32-70. 1915.
22. Evans, C. R. Effect of temperature on germination of *Amaranthus retroflexus*. Bot. Gaz. 73 (3): 213-25. 4 figs. 1922.
23. Flemion, Florence. Dwarf seedlings from non-after-ripened embryos of *Rhodotypos kerrioides*. Cont. Boyce Thompson Inst. 5 (1): 161-65. 3 figs. 1932.
24. Gardner, F. E. Composition and growth initiation of dormant Bartlett pear shoots as influenced by temperature. Plant Physiol. 4 (4): 405-34. 9 figs. 1929.
25. Gardner, W. A. Effect of light on germination of light-sensitive seeds. Bot. Gaz. 71: 249-88. 1921.
26. Garner, W. W., and Allard, H. A. Effects of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agric. Res. 18: 553-606. 1920.
27. Gassner, G., and Rabien, H. Weiters Untersuchungen zur Frage des Fröhntreibens durch gasförmige Blausäure. Die Gartenbauwissenschaft. 1: 385-402. 1928.
28. Giersbach, J., and Crocker, W. Germination and storage of wild plum seeds. Contr. Boyce Thompson Inst. 4: 39-51. 1 fig. 7 tables. 1932.
29. Harvey, R. B. Length of exposure to low temperature as a factor in the hardening process in tree seedlings. Jour. Forest. 28 (1): 50-53. 1930.
30. Holttum, R. E. On periodic leaf-change and flowering of trees in Singapore. Gardens' Bull. Straits Settlements 5 (7/8): 173-206. 1931. Biol. Abst. 6 (11): 24427.

31. Horne, W. J., Weldon, G. P. and Babcock, E. B. Resistance of peach hybrids to an obscure disease in Southern California. Jour. Hered. 17: 98-104. 1926.
32. Howard, W. L. An experimental study of the rest period in plants. Pot grown woody plants. Univ. Mo. Coll. Agric. Exp. Sta. Res. Bull. 16. 1915.
33. _____. An experimental study of the rest period in plants. Physiological changes accompanying breaking the rest period. Univ. Mo. Coll. Agric. Exp. Sta. Res. Bull. 21. 1915.
34. Ikeda, Shohgoroh. Influence of temperature on the budding of mulberry trees. Bull. Sericult and Silk-Indust. (Sanshi-gaku Zasshi) 5 (1): 1-5. 1932. (In abstract.)
35. Johannsen, W. Das Aethewerfahren beim Frühtreiben. II. Aufl. Jena. 1906.
36. Kendeigh, S. C. A study of Merriam's temperature laws. The Wilson Bulletin 44 (3): 129-43. 1932.
37. Kraus, E. J., and Kraybill, H. R. Vegetation and reproduction with special reference to the tomato. Oregon Agric. Exp. Sta. Bull. 149. 1918.
38. Lamb, G. N. A calendar of the leafing, flowering, and seed-ing of the common trees of Eastern United States. Monthly Weather Rev. Suppl. II. 1915.
39. Lefebure, E. A. Experience sur la germination des plants. 1398. Strasbourg, 1801.
40. Lehenbauer, P. A. Growth of maize seedlings in relation to temperature. Physiol. Res. 1: 247-88. 1914.
41. Livingston, B. E. Physiological temperature indices for the study of plant growth in relation to climatic conditions. Physiol. Res. 1: 399-420. 1916.
42. Livingston, B. E., and Livingston, G. J. Temperature co-efficients in plant geography and climatology. Bot. Gaz. 56: 349-75. 1913.
43. MacDougal, D. T. The temperature of the soil. Jour. N. Y. Bot. Garden. 3: 125-31. 1902.
44. _____. Lengthened growth periods and continuous growth. Proc. Amer. Philosoph. Soc. 69 (6): 329-45. 1930.
45. MacLagan, J. F. A. Date of flowering as affected by climatic temperature. Plant Physiol. 8 (3): 395-423. 8 figs. 1933.
46. Matthaei, G. L. C. Experimental researches on vegetable assimilation and respiration. Phil. Trans. Roy. Soc. (B). 197: 47-105. 1904.
47. Moshkov, B. S. Photoperiodicity of certain woody species. Bull. Appl. Bot. Genet. and Plant Breeding. 23 (2): 479-510. 13 figs. 1930. Russian with English summary.

48. Oettingen, A. J. von. Phänologie der Dorpater Lignosen. Arch. für die Naturk. Liv. Esth. und Kurlands 8 (3): 1-112. 1879.
49. Pack, D. A. After-ripening and germination of Juniperus seeds. Bot. Gaz. 71: 32-60. 1921.
50. _____. Chemistry of after-ripening, germination, and seedling development of Juniper seeds. Bot. Gaz. 72: 139-50. 1921.
51. Peretolein, K. Die Änderungen von Reservestoffen bei unseren Bäumen in der Winterruheperiode. Mittell. des Petersburg. Forst. Inst. 11: 3-42. 1904.
52. Rose, R. C. After-ripening and germination of seeds of Tilia, Sambucus, and Rubus. Bot. Gaz. 67: 281-308. 1919.
53. Sachs, Julius. Physiologische untersuchungen über die Abhängigkeit der Keimung von der Temperatur. Jacob. Wiss. Bot. 2: 338-77. 1860.
54. Sanderson, E. D., and Peairs, L. M. The relation of temperature to insect life. New Hampshire Coll. Agric. Exp. Sta. Tech. Bull. 7. 125 pp. 1913.
55. Seeley, D. A. Relation between temperature and crops. Monthly Weather Rev. 45: 354-59. 1917.
56. Shelford, V. E. Methods for the experimental study of the relation of insects to weather. Jour. Econ. Ent. 19 (2): 251-60. 1926.
57. _____. Laboratory and field ecology. Chaps. vi and vii. Williams and Wilkins. Baltimore, 1929.
58. _____. Phenology and one of its modern descendants. Quart. Rev. Biol. 5 (2): 207-16. 1930.
59. _____. Life zones, modern ecology, and the failure of temperature summing. The Wilson Bulletin 44 (3): 144-57. 1932.
60. Shreve, E. B. A thermo-electric method for determination of leaf temperature. Plant World 22: 100-104. 1919.
61. Shreve, F. The role of winter temperatures in determining the distribution of plants. Amer. Jour. Bot. 1: 194-202. 1914.
62. Smith, I. W. Phenological dates and meteorological data recorded by Thomas Mikesell between 1873-1912, at Wauseon, Ohio. U. S. Dept. of Agric. Mo. Weath. Rev. Suppl. II. 1915.
63. Stahl, E. Ueber bunte Saubblätter. Ann. Jard. Beritzenzog. 13: 153. 1896.
64. Strausbaugh, P. D. Dormancy and hardiness in the plum. Bot. Gaz. 71: 337-57. 1921.

65. Ursprung, A. Die physikalischen Eigenschaften der Laubblätter. Bibliotheca Botanica 12 (Heft 60): 68. 1903-1904.
66. Welden, G. P. On delayed foliation of peach. Pacific Rural Press. 122: 6, 10. 1926.
67. Whitten, J. C. Winter protection of the peach. Bull. 38. Missouri Agric. Exp. Sta. April, 1897.
68. _____. Preventing frost injuries by whitening. Pacific Rural Press. 60: 276. 1900.
69. Wiegand, K. M. Some studies regarding the biology of buds and twigs in winter. Bot. Gaz. 41: 373-424. 1906.

EXPLANATION OF PLATE I

- A. Plant never chilled. Etherized with 1.0 cc. per liter of air on March 3, 1931. Started leafing March 12.
- B. Plant never chilled. Etherized with 0.5 cc. per liter of air on March 3, 1931. Started leafing March 11.
- C. Plant from outdoors brought in and placed with plants A and B on March 3, 1931. Not etherized. Started leafing March 11.
- D. Plant from outdoors placed in 25° C. and darkness on February 18. Started leafing on March 2.
- E. Plant from outdoors placed on 30° C. and darkness on February 18. Started leafing March 8.

This photograph was taken March 17, 1931.



PLATE I

